

COMPARATIVE CRANIAL MORPHOLOGY
OF RECENT AND FOSSIL TURTLES

EUGENE S. GAFFNEY

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 164 : ARTICLE 2 NEW YORK : 1979

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EUGENE S. GAFFNEY

Associate Curator, Department of Vertebrate Paleontology

The American Museum of Natural History

Adjunct Professor, Department of Geological Sciences

Columbia University

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AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 164 : ARTICLE 2 NEW YORK : 1979

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 164, article 2, pages 65-376, figures 1-273, table 1

Issued September 20, 1979

Price: \$19.60 a copy

ISSN 0003-0090

CONTENTS

Abstract	69
Introduction	69
Organization	70
Terminology	70
Figures	70
Abbreviations	71
Dermal Roofing Elements	72
Nasal	72
Prefrontal	73
Frontal	75
Parietal	77
Jugal	79
Quadratojugal	80
Squamosal	81
Postorbital	82
Temporal Emargination	83
Palatal Elements	86
Premaxilla	86
Maxilla	87
Vomer	91
Palatine	93
Palatoquadrate Elements	94
Quadrate	94
Epipterygoid	97
Pterygoid	98
Braincase Elements	107
Supraoccipital	107
Exoccipital	109
Basioccipital	112
Prootic	115
Opisthotic	135
Basisphenoid	136
Cavum labyrinthicum	172
Cavum acustico-jugulare	191
Lower Jaw Elements	213
Dentary	213
Angular	216
Surangular	216
Coronoid	217
Articular	217
Prearticular	217
Splénial	218
A Review of Previous Work on Turtle Skull Morphology with Literature References to Turtle Skull Figures and Works of Systematic Interest	219
Family Proganochelyidae	225

Family Pelomedusidae	228
Family Chelidae	230
Families Glyptopsidae and Baenidae	233
Families Kinosternidae and Dermatemydidae	234
Families Trionychidae and Carettochelyidae	237
Family Plesiochelyidae	281
Family Protostegidae	281
Family Toxochelyidae	285
Family Dermochelyidae	285
Family Cheloniidae	287
Family Chelydridae	293
Family Emydidae	297
Family Testudinidae	322
Genera at Present <i>Incertae Sedis</i>	326
Glossary	356
Acknowledgments	364
Index to Genera	364
Literature Cited	367

ABSTRACT

Comparative descriptions of the cranial morphology in living and extinct turtles are presented in this paper. Descriptions are arranged by bone rather than by taxon and attempt to document the types and degrees of differences in cranial structures within the Testudines, emphasizing features of systematic interest. Developmental information is also included. 273 figures supplement the text. About half of these figures show detailed internal morphology and include comparative series showing horizontal and sagittal sections, and oblique views of ear regions for each of the living families of turtles as well as for those extinct families where this information is available. Additional figures, some of which are taken

from the literature, show disarticulated elements, inner ear regions, arterial and nerve foramina and canals, and basicranial morphology. The other half of the figures are dorsal, lateral, and ventral views (also occipital views in many cases) of the skull in nearly all living genera of turtles and many extinct genera. The higher category classification used is that developed by Gaffney (1975d) and no taxonomic novelties are announced. A section of text provides a brief literature review of chelonian systematics and cranial morphology and a listing (by family) of useful turtle skull illustrations from the literature. A revised glossary of anatomical terms and an index are included.

INTRODUCTION

"Certainly the braincase is analogous to the commode; both serve a seemingly indispensable function, and thus have, as a result, remained in all particulars in a pristine and unmodified condition (at least as regards their structure) through a grievous long period of time on Earth. . . ."

—Cuthbert Tomlinson Tedwelle, Esq., 1678
Tome II, *Animalium Frustratum*, Part II:
"On the skulls of divers and sundry
creatures of the Grotzwell bogs,
Marston-on-Kent"

"Prithee, is it perchance possible that the contents of his skull are analogous to the content of the commode?"

John Jones, 1679
Vol. I: "On the skull of C. Tomlinson Tedwelle"

Morphological description can be among the most tedious, tiresome, and, most unfortunately, the least useful of the biological literature. "Pure" anatomical information that is supposedly gathered without regard to some theory or idea often inspires none. Nonetheless, the anatomical literature, particularly the well-illustrated papers, form the core against which we must test most systematic and functional hypotheses. With this in mind I present yet another bone by bone account of detailed morphology, this time in the hope that it will be of particular use to turtle systematists.

Most of the classic works on vertebrate anat-

omy tend to overgeneralize differences within groups in order to make teaching morphology easier and ease comparisons between groups. Turtles have often been characterized as having a uniform structural plan but the magnitude of variation, particularly in the skull, has rarely been emphasized or dealt with. Nonetheless, this variation is potentially of considerable interest, both systematically and functionally. This paper attempts to describe the differences in skull morphology among known fossil and Recent turtles, with particular emphasis on features that are or have been considered to be of functional or systematic interest within the

Testudines rather than between turtles and other vertebrates.

ORGANIZATION

I have chosen to organize the morphological information by bone rather than by presumed functional units or by other morphological criteria. The bones are generally arranged in developmental units. If a particular structure is formed by more than one bone it is discussed only under one bone but references to the discussion may be found under the other bones forming the same structure. Two basicranial regions, the *cavum acustico-jugulare* and *cavum labyrinthicum*, are particularly complex and are described in a separate section rather than under individual bones.

The descriptive sections are divided into portions dealing with contacts, development, and structures in order to make reference easier. However, it has been impossible to strictly separate many topics and in some cases (such as the epipterygoid) a meaningful separation was not possible. The reader should also briefly peruse other subdivisions of a bone even when interested only in contacts, for example, to be sure that relevant topics are not discussed elsewhere. I have made a strong effort to cross reference as many topics as possible although a certain amount of repetition may have resulted.

The morphology sections are followed by a multipurpose chapter that begins with a literature review of turtle skull morphology. The bulk of the chapter, however, consists of a family by family compilation of references to turtle skull figures in the literature. Under each family heading there is also a review of important papers on the systematics of each group and a statement regarding the particular scheme I have followed here. The higher category classification I use is developed by Gaffney (1975d) and the reader should see that paper for further information. The cladogram depicting the main features of my phylogenetic hypotheses is repeated here as figure 113 for the reader's convenience. I do not believe that a morphological paper of the sort presented here is the place for new phylogenetic ideas or new taxa. Therefore, no systematic novelties either

in the form of new higher categories or radical changes of family content are given.

TERMINOLOGY

I use the Parsons and Williams' (1961) terms as developed by me (1972b). For the reader's convenience a revised version of that Glossary is included. The use of a formal nomenclature makes it difficult for the worker beginning anatomical studies, but I think the initial unfamiliarity and cumbersome nature of the terms is outweighed by their usefulness. A latinized terminology allows ready translation into other languages, formal definition, and use of the terms reduces ambiguity between authors and, in any case, anglicized versions are usually no shorter nor easier to use in the long run. The Glossary also serves the purpose of providing a cross reference for figures of particular structures that appear in this paper.

FIGURES

In my opinion, the illustrations are the most useful and most used part of anatomical literature. Text may clarify and compare features but the accuracy and clarity of figures bear a great deal of weight. With this in mind I have compiled what I consider to be some of the most useful figures from the literature and have added new ones for balance. The figures are organized in two main sections: Detailed or comparative morphology figures (1 to 112) appear first—followed by overall views of skulls (113 to 273), systematically arranged. The comparative morphology section attempts to follow the order of bones in the text but because most of the figures involve more than one bone, many compromises were necessary. A brief summary of the organization of these figures seems appropriate. Figures 1-8, skull roof; figure 9, structures seen in ventral view; figures 10-19, quadrate, ethmoid region, middle ear; figures 20-29, pterygoids; figures 30-36, arteries and canals; figures 37-43, primary neurocranium; figure 44, basisphenoid; figures 45-52, ear region and basicranium; figures 53-65, dorsal views of horizontally sectioned skulls; figures 66-83, sagittal sections; figures

84-102, middle ear stereophotographs; figures 103-109, series taken from Ogushi (1911) illustrating various cranial regions; figure 110, chelids; figures 111-112, lower jaws.

A number of the above topics overlap and use of the Glossary as well as a search through the figures may be necessary at times.

For a brief introduction to turtle skull morphology the reader should examine the following *Chelydra* figures (preferably with a specimen in hand): 9 (palate), 11 (ethmoid), 33 (arterial canals), 37 and 39 (primary braincase), 41 (occiput), 50 and 87 (ear region), 64 (frontal section), 76 (sagittal section), 95 (stereo of ear region), 217 (entire skull).

The second half of the figures are organized by family in the same order as that in the literature review chapter. Within the families the genera are arranged alphabetically, the generic index is helpful to locate desired figures (when looking for a figure of the entire skull, look only from figs. 114-273).

The figure legends in general contain whatever data are readily available about the specimen (figures from the literature usually lack data and I have made no great effort to obtain information on these specimens). In most cases the identification is followed by the museum number and the midline length of the specimen from premaxilla to condyle. Family designation, age (if other than Recent), and locality are also stated where known. The choice of forms to be illustrated was difficult. In the morphological section I try to illustrate comparative series using at least one specimen from each family, particularly those that are not monotypic. In many cases the availability (or lack of it) of specimens for sectioning or disarticulation determined what particular genera were actually figured. In the systematic section I approach my original goal of figuring all living genera and well-known fossil genera, but unfortunately I do not attain it. The result may be considered unbalanced.

Although paleontologists have published specimen numbers of figured specimens for some time due to the supposed uniqueness of their material—herpetologists, particularly those concerned with anatomical work—rarely indicate the numbers of figured specimens. There is

a fair amount of instability in the recognition of Recent turtle species, and I urge future workers to explicitly state specimen numbers of figured specimens and to catalogue and retain dissected material.

ABBREVIATIONS

ANATOMICAL

ang, angular	pal, palatine
art, articular	pf, prefrontal
bo, basioccipital	pm, premaxilla
bs, basisphenoid	po, postorbital
cor, coronoid	pr, prootic
den, dentary	pra, prearticular
epi, epipterygoid	pt, pterygoid
ex, exoccipital	qj, quadratojugal
fr, frontal	qu, quadrate
ju, jugal	so, supraoccipital
mx, maxilla	sp, splenial
na, nasal	sq, squamosal
op, opisthotic	sur, surangular
pa, parietal	vo, vomer

INSTITUTIONAL

AMNH, The American Museum of Natural History, New York
AMS, Australian Museum, Sidney
BMNH, British Museum (Natural History), London
CM, Carnegie Museum, Pittsburgh
FMNH, Field Museum of Natural History, Chicago
HUB, Museum für Naturkunde, Humboldt Universität, Berlin
IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels
KU, University of Kansas, Natural History Museum, Lawrence
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
MH, Natural History Museum, Basel
NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
PU, Princeton University, Princeton
ROM, Royal Ontario Museum, Ottawa
SM, Solothurn Museum, Solothurn
SMM, Science Museum of Minnesota, Saint Paul
TM, Teyler Museum, Haarlem
UCMP, Museum of Paleontology, University of California, Berkeley
UMMP, Museum of Paleontology, University of Michigan, Ann Arbor
UT, Slide Collection, Department of Zoology, University of Toronto
YPM, Yale Peabody Museum, New Haven

DERMAL ROOFING ELEMENTS

NASAL

Figures 1, 3, 12

DEVELOPMENT: Nasals occur only in chelids among Recent turtles. As development of a chelid has never been reported, there is no information on nasals.

CONTACTS: Nasals are present only in chelids (except *Chelus*) among Recent forms but occur more commonly in fossil groups. The nasals of chelids (figs. 142-149) have a long medial suture with the frontals, which may prevent sagittal contact of the nasals (as in *Chelodina*). Posterolaterally, the maxilla contacts the nasals and the posterior limits of the nasals reach the prefrontals. In toxochelyids (Zangerl, 1953) and plesiochelyids (Gaffney, 1975b) the nasals meet sagittally in a short suture and have a broad transverse contact with the prefrontals posteriorly. Laterally, there is a short suture with the maxilla. Chelosphargine protostegids also have nasals (Zangerl, 1953) and one form, *Rhinochelys*, (Collins, 1970; Moret, 1935) has an unusual amount of variation in the contacts. The nasal usually meets the frontal, prefrontal, and maxilla but in some cases each bone may be nearly excluded from the nasal by the expansion of the other two. Baenoids (fig. 1) have nasals (Gaffney, 1972a; Evans and Kemp, 1975) which meet sagittally, contact the frontal posteriorly, and contact the maxilla laterally (except in *Chisternon*). The nasals of *Solnhofia* (Gaffney, 1975c) have a mutual sagittal suture, a lateral suture with the maxilla, and a posterior contact with the prefrontals. *Proganochelys* has nasals (Jaekel, 1916; Parsons and Williams, 1961) but their contacts as described are questionable. Parsons and Williams (1961), however, have noted that the premaxillae send processes dorsally to articulate with the nasals and divide the apertura narium externa along the midline.

STRUCTURES: The nasals are small quad-

rilateral elements forming the roof of the fossa nasalis and the dorsal margin of the apertura narium externa. *Proganochelys* (figs. 114, 116) has an apertura narium externa that is divided by dorsal processes of the premaxillae (Parsons and Williams, 1961, p. 91). Meiolaniids and

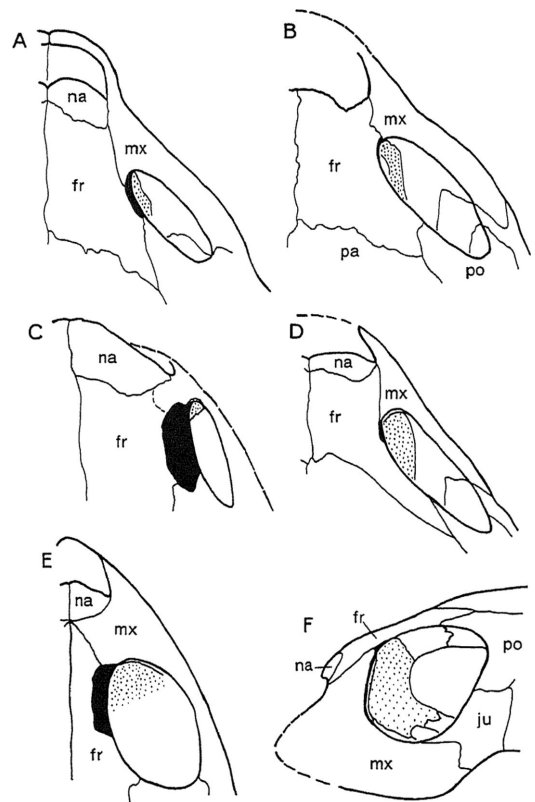


FIG. 1. Anterior skull roof morphology in baenoids. Dorsal lappet of prefrontal in black, descending process of prefrontal stippled. A. *Eubaena cephalica*. B. *Stygiochelys estesi*. C. *Hayemys latifrons*. D. *Chisternon undatum*. E. *Glyptops plicatus*. F. *Chisternon undatum*. A-E. Dorsal views of right side of skull; F. Lateral view of left side of skull.

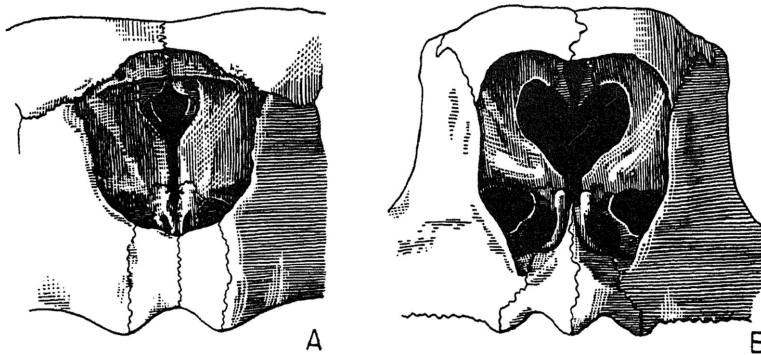


FIG. 2. Comparison of width of the fissura ethmoidalis: A. Typical Emydidae (*Clemmys insculpta*). B. Typical Testudinidae (*Gopherus agassizii*). Both figures are anterior views through the apertura narium externa and show the descending processes of the prefrontals forming the fissura ethmoidalis (from Loveridge and Williams, 1957).

Kallokibotion also have divided narial openings but it is not known whether the premaxillae or nasals form the septum in these groups. In some baenids (*Baena* and *Palatobaena*) the nasals and frontals are apparently fused.

PREFRONTAL

Figures 1-4, 66-80

DEVELOPMENT: The prefrontal is a membrane bone that exhibits very much the same relations in the chondrocranium as in the adult skull. A well-developed vertical process occupies the anterior wall of the orbit and a horizontal process lies on the skull roof anterior to the frontal. There is little embryological evidence to support the contention that this bone is homologous to the lacrimal of other reptiles or that the lacrimal is incorporated into this bone (see section below concerning previous identifications of a "lacrimal" in baenids).

CONTACTS: In all turtles that I know the prefrontal has a long anterolateral suture with the maxilla. There is also consistently a suture with the frontal usually along the posterior edge of the prefrontal. This last contact is commonly reduced to a posteromedial suture by the addition of the postorbital posterolaterally as in most living cryptodires. Living cryptodires and

pelomedusids have a medial contact of both prefrontals, but in chelids and baenids the prefrontals do not meet in the midline, this last condition presumably being the more primitive.

Cryptodires have a well-developed ventral or descending process of the prefrontal that articulates with elements of the palate (figs. 2, 76). This process usually contacts the vomer ventromedially and the palatine posteroventrally. In trionychids the palatine articulation is lost and the vomer articulation may also be lost (*Chitra* and *Cycloderma*). In all pleurodires the prefrontal lacks a contact with the vomer and only in *Bothremys* (Gaffney and Zangerl, 1968) is the prefrontal known to have a well-developed contact with the palatine. The condition in *Bothremys* is probably secondary and due to the unusual and highly specialized nature of the palate. However, a slight prefrontal-palatine contact exists in some specimens of *Emydura* and *Pelusios* as an individual variation. In chelids, most baenids, toxochelyids and various Mesozoic forms there is an anterior contact with the nasal.

STRUCTURES: The paired prefrontals (figs. 4, 66, 78) usually consist of two plates, a horizontal and a vertical one, meeting at right angles in the anterodorsal corner of the orbit. The dorsal plate in most turtles is expanded anteriorly and medially in comparison to other rep-

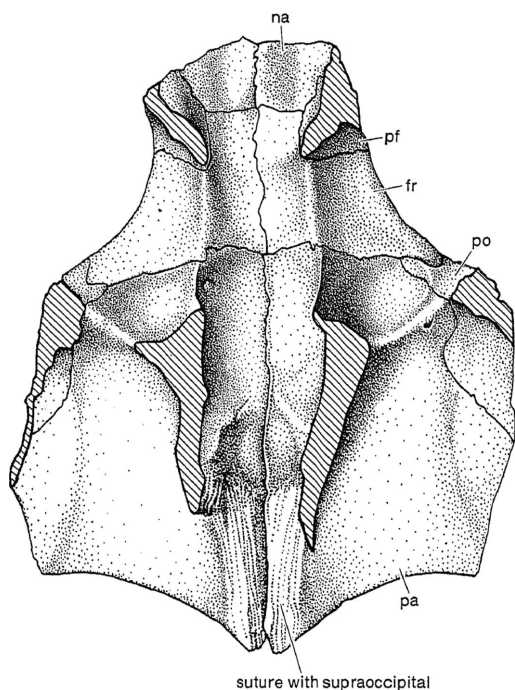


FIG. 3. Ventral view of skull roof in *Chisternon undatum* (YPM 3930), Baenidae, Bridger B, Bridger Formation, Eocene, Granger, Wyoming. Nasals are well developed and separate the dorsal lappets of the prefrontals in contrast to the condition seen in figure 4. Supraoccipital bone is missing and the irregular stipple indicates broken surfaces that are not in the same plane.

tiles and occupies the position of nasals in most living turtles (compare figs. 3 and 4). The dorsal plate forms the dorsal edge of the apertura narium externa in these forms and most of the roof of the fossa nasalis. The living chelids and fossil baenids have a relatively small dorsal plate that does not meet the other prefrontal in the midline and retain nasal bones in most cases. Presumably this is the primitive condition and, if so, the pelomedusids and eucryptodires have independently evolved an expanded dorsal plate meeting in the midline as well as losing the nasal independently.

The vertical descending plate of the prefrontal is characteristic of most cryptodires and generally occupies the position of the lacrimal

in other reptiles. It forms the following structures (fig. 66): a wall between the fossa nasalis and fossa orbitalis, the anterior margin of the foramen interorbitale, the dorsolateral margin of the fissura ethmoidalis, and the dorsal margin of the foramen orbito-nasale. Although a certain amount of size variation exists in all these structures, the fossa nasalis and fissura ethmoidalis become particularly large in testudinids, whereas emydids characteristically have a very narrow fissura ethmoidalis.

The descending process is variably reduced in trionychoids (see discussion above). Some, such as *Trionyx*, have a medial contact with the vomer; others, such as *Chitra*, lack a vomerine suture and all lack a contact with the palatine.

Pleurodires (figs. 67-70) are usually considered to lack a descending process of the prefrontal (Romer, 1956, p. 514) but in *Bothremys*

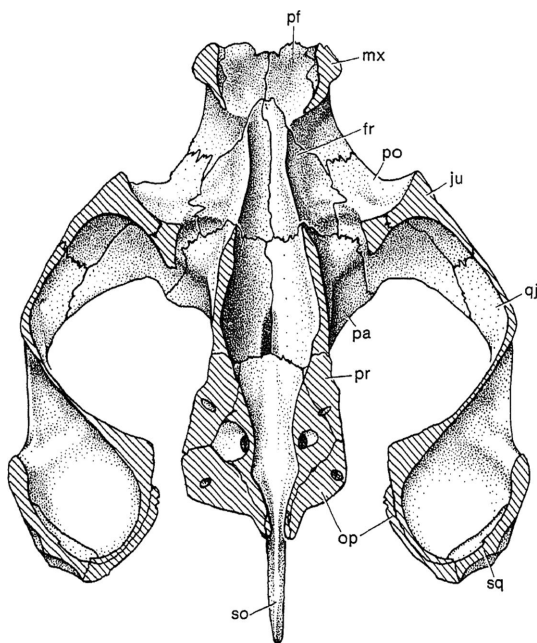


FIG. 4. Ventral view of skull roof in *Pelusios* sp. (AMNH 10062), Pelomedusidae, Faradje, Haut-Zaire, Zaire. Nasals are absent but there are expanded dorsal lappets of the prefrontals that meet in the midline in contrast to the condition seen in figure 3. The irregular stipple indicates the sectioned surface that is in the same horizontal plane.

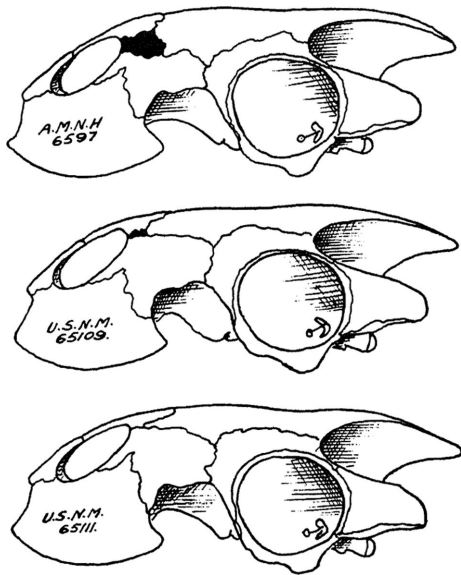


FIG. 5. Variation in postorbital size in *Podocnemis expansa*, Pelomedusidae. Uppermost figure is the usual condition whereas the lower two show less exposure of the postorbital (solid black) on the dorsal surface (Ruckes, 1937b).

and occasional specimens of living pleurodires (*Emydura* sp., AMNH 72418; *Pelusios* sp., AMNH 10053) the prefrontal contacts the palatine. In the above instances, however, the contact is due to a well-developed anterior extension of the palatine, and there is no indication of a vomerine contact nor of the formation of a foramen orbito-nasale as in cryptodires. Pleurodires, then, do lack the sort of prefrontal process found in cryptodires.

Hay (1904, 1905, 1908a) reported the presence of a bone in the anterior orbital margin of *Eubaena cephalica*, *Baena arenosa*, and *Chisternon undatum* which he identified as the lacrimal. Hay gave no reason for the identification but presumably based it on the similarity in morphology and position between this bone and the lacrimal in mammals. In all living cryptodires the bone in the anterior wall of the orbit is the ventral process of the prefrontal. In baenids Hay identified as the prefrontal what I have identified as the frontal (Gaffney, 1972a, p. 288, fig. 56). Therefore, the bone in the

position of the ventral process of the prefrontal he believed must be the lacrimal. The error actually began with Hay's misinterpretation of the parietal as the parietal and frontal fused together. The element anterior to the two fused bones should have been the prefrontal and the result was an extra bone at the front of the skull, the "lacrimal." In regard to the position of the "lacrimals" Hay stated (1905, p. 139): "These occupy the position of those processes of the prefrontals which in other turtles descend to meet the vomer." In fact, the "lacrimal" has the following features in common with the prefrontal of living cryptodires:

- (1) articulates with the vomer ventromedially
- (2) borders the foramen orbito-nasale ventrolaterally
- (3) meets the palatine between the two above structures
- (4) has a long suture with the maxilla along the anterior border of the fossa orbitalis.

From these features I conclude that baenids lack a lacrimal and that, with the possible exception of *Proganochelys*, there are no turtles with lacrimals.

FRONTAL

Figures 1, 3, 4, 6, 66-80

DEVELOPMENT: As is the case with the parietal, the frontal appears in the embryo along the side of the braincase and only later comes to roof the skull.

CONTACTS: The frontal is a flat bone lying in the anterior part of the skull roof on either side of the midline. In living turtles the most common contacts are as follows: prefrontal anteriorly, postorbital laterally, parietal posteriorly, and the other frontal medially. The baenoids, plesiochelyids, toxochelyids, chelosphargine protostegids, and some other Mesozoic forms usually have a broad, anterior contact with the nasal. Chelids also have a nasal contact but in this group the nasal lies along the anterolateral edge of the frontal. Baenoids also have a well-developed contact with the dorsal process of the maxilla, a contact that is also found in *Trionyx subplanus* (Siebenrock, 1897, p. 276; fig. 27 "*Dogania*

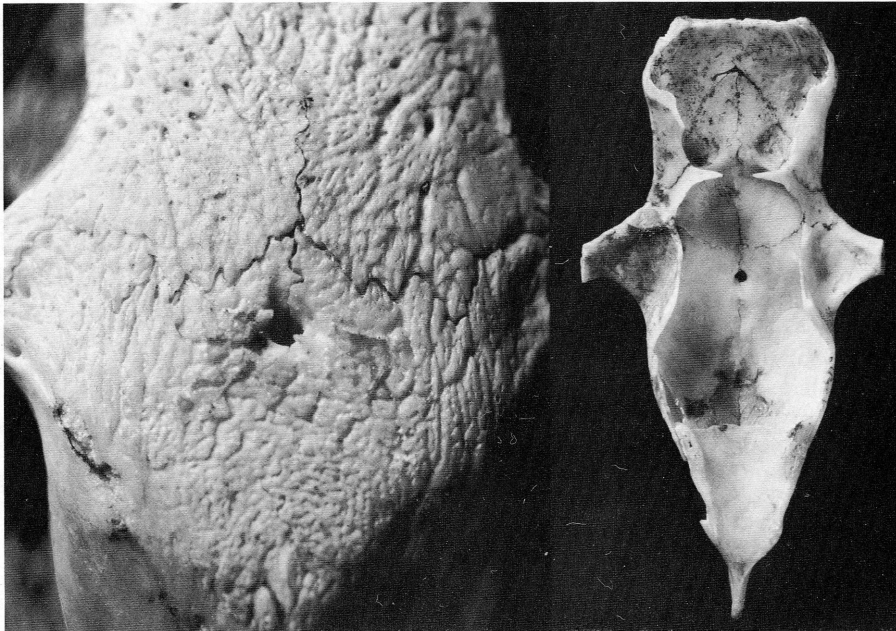


FIG. 6. A parietal foramen in the parietal bones of *Geochelone denticulata*, Testudinidae. The foramen is usually absent but rarely occurs in turtles as an individual variation. Left, dorsal view of skull; right, ventral view of skull roof also showing large fossa nasalis and ventromedial frontal processes, both characteristic of this family (from Zangerl, 1957; I am indebted to Dr. Zangerl for new prints of these figures).

subplana”) although it is quite small in that form. In *Chelodina* the frontals are fused in the midline.

STRUCTURES: The frontal (figs. 3, 4, 66, 78) participates in the formation of the fossa orbitalis, the sulcus olfactorius and the fossa nasalis. The roof of the orbit is covered by the lateral portion of the frontal and the frontal often forms the dorsal part of the orbital margin. However, this is not always the case and in many forms (e.g., *Dermochelys*, *Chelydra*) the prefrontal and postorbital meet on the orbital margin to prevent exposure of the frontal. This condition may be subject to individual variation in which case the frontal is exposed in some individuals and not in others as is reported in *Chelonia mydas* (Boulenger, 1890, p. 618) and *Emys orbicularis* (Siebenrock, 1897, p. 276). In some forms, such as *Staurotypus*, the frontal is widely separated from the orbital margin and is relatively small in size.

The ventral surface of the frontal has a para-

sagittal ridge, that separates the sulcus olfactorius medially from the fossa orbitalis laterally. The sulcus transmits the olfactory (I) nerve from the cavum cranii into the fossa nasalis. In most turtles the sulcus is relatively narrow but in some forms (e.g., *Carettochelys*) the sulcus olfactorius may be as wide as the more posterior portion of the cavum cranii. The ridge forming the lateral margin of the sulcus olfactorius may develop ventromedial processes (e.g., *Geochelone*, *sensu* Loveridge and Williams, 1957) or the whole ridge may extend ventromedially (e.g., *Chelodina*) resulting in the development of a partial bony tunnel. Much of the cartilaginous planum suprasetale of the embryo persists into the adult and the dorsal Y-shaped portion of this structure completes the tunnel for the olfactory (I) nerve (Soliman, 1964, figs. 13, 24; Nick, 1912). The ventral edge of this ridge is the dorsal margin of the foramen interorbitale, the large space seen in the bony skull after the removal of the interor-

bital cartilages (the embryonic planum suprasetale and the septum interorbitale).

The frontal also forms part of the roof of the fossa nasalis. In most Recent turtles the prefrontals are greatly developed and enclose most of the fossa nasalis. However, in baenoids the prefrontals are small and the frontals do form much of the fossa nasalis roof. Chelids have a characteristic anterior frontal process that extends along the midline toward the dorsal margin of the apertura narium externa and may reach it (*Chelus fimbriata*). This process is usually flanked by a dorsal lappet of the prefrontal

for most of the length of the frontal process with the nasal lying alongside it more anteriorly.

PARIETAL

Figures 3, 4, 6, 7, 8, 66-80

DEVELOPMENT: In turtles described in the literature (*Emys*, *Chrysemys*, and *Chelonia*; see pp. 223-224) the processus inferior parietalis develops first and only later does the dorsal skull roof portion of the parietal develop. The mature chondrocrania are all open in the dorsal

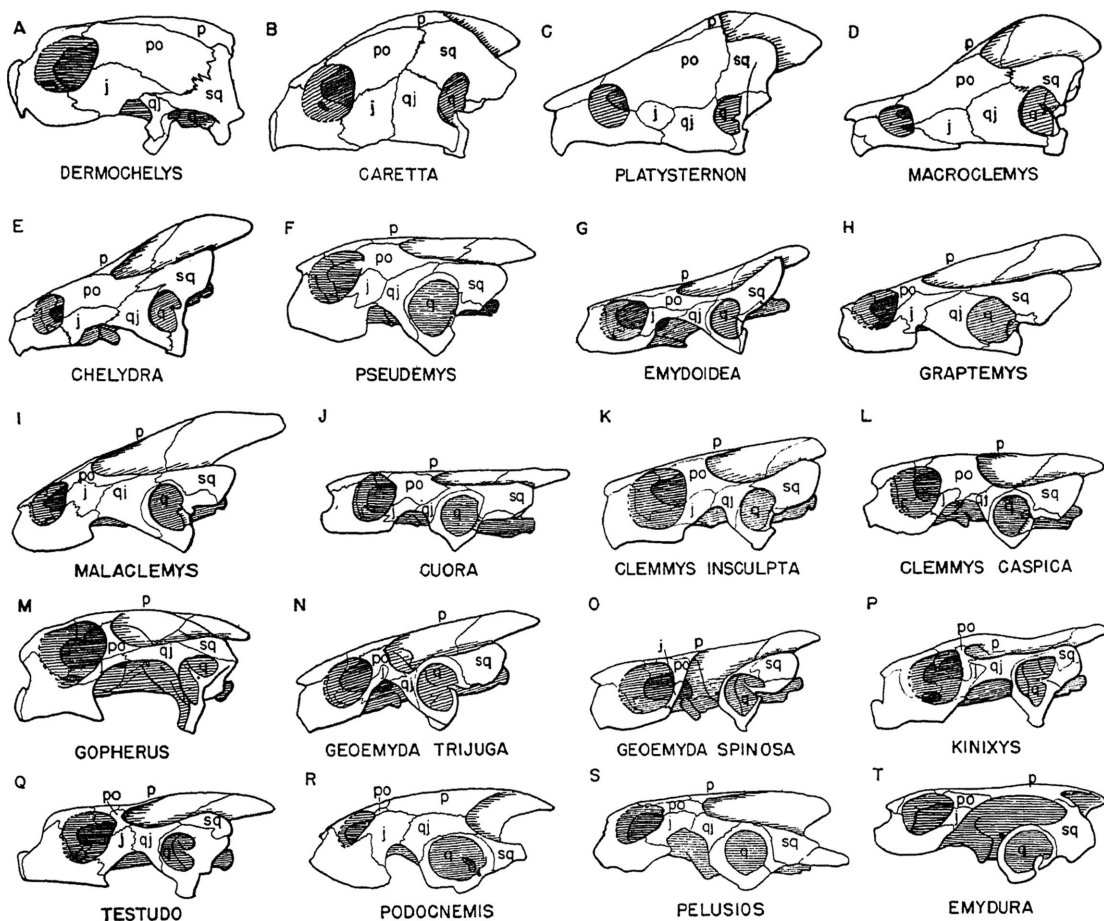


FIG. 7. Right lateral views of some turtle skulls to show types and degree of skull roof emargination (from Romer, 1956, which was based on Zangerl, 1948b).

Abbreviations: j, jugal; p, parietal; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal.

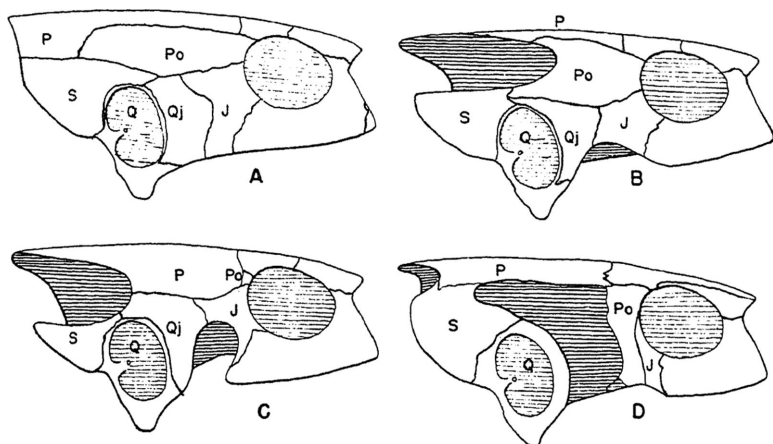


FIG. 8. Four generalized conditions of the chelonian skull roof as idealized by Zangerl (1948b). Figure A represents the "morphotype" or structural ancestor from which the other three types could be derived and is characteristic of the recent Chelonioidae; figure C is limited to the genus *Podocnemis*; figure D is typical of the Chelidae; figure B is the condition found in most other turtles.

region of the braincase. The processus inferior parietalis extends ventrally to reach the processus ascendens of the palatoquadrate (which ossifies as the epipterygoid) but lateral to the pila prootica resulting in the development of the cavum epiptericum (see cavum epiptericum under Pterygoid).

STRUCTURES AND CONTACTS: The parietal (figs. 3, 4, 67, 78) consists of two plates of bone, a dorsal horizontal plate forming much of the temporal skull roof and a ventrally directed vertical plate, the processus inferior parietalis, running parasagittally and separating the cavum cranii from the fossa temporalis. The dorsal plate always contacts the supraoccipital posteriorly, the frontal anteriorly, the postorbital anterolaterally, and the other parietal medially. In forms with a well-developed temporal roof (see Emargination, for more complete discussion) there may be a posterolateral contact with the squamosal as in Recent Chelonioidae. Chelids (except *Chelodina*) also have a parietal-squamosal contact due to the formation of a bar caused by the relative absence of posterior emargination and extreme development of cheek emargination. In some trionychids (such as *Cycloderma* and *Pelochelys*), and *Podocnemis* (*sensu* Baur, 1890) but not *Erymnochelys*

and *Peltocephalus* the parietal contacts the jugal anterolaterally. In *Podocnemis*, *Peltocephalus*, and *Erymnochelys* the parietal contacts the quadratojugal laterally. The dorsal plate reaches a large size in chelonoids, *Platysternon*, some baenids and podocnemines, and becomes reduced in some groups, such as testudinoids, chelids, and trionychids. Such forms as *Geoemyda* and *Chelodina* appear to have the most reduced dorsal plate of a parietal. In *Pseudemidura* a short process of the parietal contacts the quadrate just anterior to the squamosal.

The processus inferior parietalis is a ventrally directed parasagittal plate forming the lateral wall of the cavum cranii and a portion of the foramen nervi trigemini. The processus inferior parietalis usually has a variably developed ventral articulation with the crista pterygoidea of the pterygoid. Laterally, the processus inferior parietalis of *Gopherus* and *Testudo* (*sensu* Loveridge and Williams, 1957) overlaps the prootic and reaches the quadrate. In cryptodires the epipterygoid usually ossifies between the processus inferior parietalis of the parietal and the crista pterygoidea of the pterygoid. Usually, the epipterygoid is more extensive on the lateral surface and may allow

parietal-pterygoid contact on the medial surface. The epipterygoid in most cases is absent more anteriorly and the parietal and pterygoid may meet for a variable length. The anteroventral portion of the processus inferior parietalis contacts the palatine in a number of cryptodires and pleurodires and may reach the maxilla (*Malayemys*, for example). In trionychids, kinosternids, and some emydids the anterior portion of the processus inferior parietalis is replaced by a vertical development of the palatine bone (see Palatine).

The foramen nervi trigemini is usually formed along the posteroventral edge of the processus inferior parietalis with the epipterygoid (when present), pterygoid, and prootic usually bordering the rest of the foramen (see Prootic for main discussion of foramen nervi trigemini). In some testudinids the parietal may divide the two branches of the trigeminal nerve and each may exit in its own foramen.

The anterior edge of the processus inferior parietalis forms the posterior margin of the large foramen interorbitale. This is a paired opening found medial to the orbits and is largely filled with cartilage or membrane in life. The optic (II), oculomotor (III), trochlearis (IV) and profundus (V_1 branch of the trigeminus) nerves traverse this area. Eye muscles insert, at least in part, in this area (see cavum epiptericum in Pterygoid). Some or all of the following bones may participate in the margins of the foramen interorbitale: prefrontal, frontal, parietal, epipterygoid, pterygoid, palatine, and vomer. The fronto-parietal ridge defining the sulcus olfactorius forms the dorsal border, the prefrontal forms the anterior border, the parietal and epipterygoid the posterior border, whereas the less distinct ventral margin is formed by the pterygoid, vomer, and palatine.

JUGAL

Figures 1, 4, 7, 8, 9, 12, 53-65

DEVELOPMENT: The jugal is a membrane bone that ossifies posteroventral to the orbit.

STRUCTURES AND CONTACTS: The jugal (fig. 64, 217) is one of the main zygomatic arch elements and usually occurs just behind the

orbit. There is a dorsal suture with the postorbital and an anteroventral suture with the maxilla. The anterior edge of the jugal is usually exposed in the orbit, but in some forms (*Platysternon* and *Eubaena*, for example) the postorbital and maxilla meet in front of the jugal preventing the jugal from entering the orbital margin. A posterior contact with the quadratojugal forms the zygomatic arch and is present in all turtles (except those lacking a quadratojugal or having an extremely reduced quadratojugal as in *Terrapene carolina*).

The ventral margin of the jugal is in most cases exposed along the lateral edge of the fenestra subtemporalis and is usually involved in the development of lateral or cheek emargination. Considerable development of cheek emargination usually results in decrease in size of the jugal and it may become a small splint, as in *Geoemyda*. In some forms (for example *Chrysemys* [fide McDowell, 1964] and *Platysternon*) the maxilla and quadratojugal meet beneath the jugal to prevent ventral exposure of the jugal. *Platysternon* is somewhat unusual in that it lacks any development of cheek emargination but, nonetheless, has a reduced jugal with a postorbital-maxilla contact and quadratojugal-maxilla contact preventing exposure along the orbit and ventral cheek margin, a combination found in no other turtle.

At the anterior edge of the fenestra subtemporalis the jugal (also the postorbital in pleurodires) forms an anterior wall for the fossa temporalis inferior. The maxilla lies directly beneath the jugal in this area resulting in a straight horizontal suture at the lower margin of this anterior wall.

Most turtles have a medially directed process of the jugal that articulates with the pterygoid alone (chelydrids, some emydids) or pterygoid and palatine (kinosternids, cheloniids, *Platysternon*, *Dermatemys*, trionychids, some emydids). The medial process may reach only the palatine (for example, *Carettochelys*) or the process may not reach either bone due to reduction or absence as in *Dermochelys* and testudinids. In some emydids (such as *Malaclemys* and *Deirochelys*) there may be a short articulation with the epipterygoid.

STRUCTURES ASSOCIATED WITH THE JUGAL IN PLEURODIRES: In pleurodires (figs. 53-55) the jugal along with the postorbital make up the characteristic postorbital wall found in this group. The jugal usually forms the more lateral portions of the wall, whereas the postorbital forms the more medial area. As in cryptodires the jugal of pleurodires may reach the palatine (*Podocnemis*, *sensu* Baur, 1890) but there is always a strong contact with the anterior edge of the pterygoid, presumably to aid in support of the uniquely pleurodiran processus trochlearis pterygoidei.

The jugal and postorbital of chelids (fig. 110 and others indicated above) show some interesting features. In relatively generalized chelids, such as *Emydura*, the jugal and postorbital form a postorbital wall quite similar to that found in other pleurodires. These bones consist of two portions, a medial section exposed behind the fossa orbitalis and forming the front of the fossa temporalis inferior and a lateral portion exposed on the external surface of the skull. The morphologic series *Emydura-Chelodina-Chelus* shows a progressive posterolateral movement of the jugal and postorbital where they are exposed in the anterior wall of the fossa temporalis inferior. In *Emydura* this wall faces posterolaterally, in *Chelodina* it faces dorsolaterally, and in *Chelus* it faces dorsally. Also in *Chelus* the surface of these two bones, that in *Emydura* forms the anterior wall of the fossa temporalis inferior, lies on the external surface of the skull in *Chelus*. *Chelodina* seems to be intermediate with the wall oriented laterally but still bearing jaw muscle attachments, as in *Emydura*. In *Chelus* this wall is entirely on the external surface of the skull and bears no musculature.

Bothremys also has an unusual jugal morphology (Gaffney and Zangerl, 1968, p. 215). In this form a pair of large, ventrally open pits are developed on the triturating surface. These pits are formed primarily by the jugal in the area that in other turtles faces posteriorly into the fossa temporalis inferior. In *Bothremys* this area is greatly expanded and incorporated into the triturating surfaces. Presumably, the jugal

was covered by the horny rhamphotheca, a condition not found in any other turtle.

QUADRATOJUGAL

Figures 7, 8

DEVELOPMENT: The quadratojugal is a membrane bone that ossifies as a flat plate fairly late in the forms described: *Emys* (Kunkel, 1912), *Chrysemys* (Shaner, 1926). Some species (see below), in which the quadratojugal is lost apparently due to cheek emargination might utilize neoteny as a mechanism.

STRUCTURES AND CONTACTS: The quadratojugal is absent in those turtles with extensive cheek emargination, namely the Chelidae and some Emydidae. The chelid *Pseudemydura*, however, has a well-developed temporal roof but still lacks a quadratojugal, suggesting that the skull roof in this form may be secondarily enlarged from an extensively emarginated ancestor lacking a quadratojugal. In the emydids, *Cuora galbinifrons* (*fide* Bourret, 1941), *Cuora flavomarginata* (*fide* McDowell, 1964), *Hieremys annandalii*, and some species of *Geoemyda* (*G. depressa*, *G. grandis*, *G. leyensis*, *G. silvatica*, and *G. spinosa*, which constitutes *Heosemys* of McDowell, 1964) all lack the quadratojugal. According to McDowell the other species of *Geoemyda* (mostly equivalent to *Rhinoclemys* and *Melanochelys* of McDowell) have a quadratojugal loosely attached and subject to loss in the dried skull. In this regard McDowell's discussion of the quadratojugal (=squamosal of McDowell) in *Notochelys* is of interest: "Malcolm Smith says the 'quadratojugal' may be present or absent, and the statement is repeated here, although the two young Sumatran individuals I have examined both had the bone. I am very skeptical of the statements in the literature about variable occurrence of the squamosal [quadratojugal] in this group of turtles because the bone is so loosely attached that it is easily lost in preparation and leaves little or no mark on the quadrato to hint at its former presence. Proof of individual variability in presence of this bone based on alizarin clearings or dissection of

whole heads needs to be presented" (McDowell, 1964, p. 266). In some species of *Terrapene* (Taylor, 1895; Zangerl, 1948b; Milstead, 1969) the quadratojugal is reduced and in *T. ornata* and *T. nelsoni* (taxonomy *vide* Milstead, 1969) it is lost entirely. Milstead also reported that within some subspecies of *Terrapene carolina* the quadratojugal may be present, cartilaginous, or absent.

The contacts of the quadratojugal are somewhat variable but there is always a posterior semicircular indentation for the quadrate. In most turtles the quadratojugal also contacts the jugal anteriorly, the postorbital anterodorsally, and the squamosal posterodorsally. In some forms the quadratojugal may reach the maxilla (*Malaclemys*, *Chrysemys*, kinosternids, *Platysternon*) or the parietal (*Podocnemis*, *Peltocephalus*, *Erymnochelys*). A quadratojugal-postorbital contact is absent in *Podocnemis* (but not in *Peltocephalus* and *Erymnochelys*) and trionychids, and the squamosal contact may be lost with well-developed posterior emargination (for example, *Cuora trifasciata*). In some specimens of *Terrapene carolina* the quadratojugal appears to be attached only to the quadrate, having lost all other contacts due to emargination (Taylor, 1895). The quadratojugal of *Dermochelys* is also reduced but not from emargination. The jugal of *Dermochelys* is relatively large and occupies areas that are occupied by the quadratojugal in other forms.

HOMOLOGY: Although it is not my intention to present a general review of bone homology between turtles and other reptiles, McDowell's (1964) recent use of "squamosal" for quadratojugal of other authors and "supratemporal" for squamosal of other authors requires comment, particularly as some workers (e.g., Milstead and Tinkle, 1967; Milstead, 1969) have adopted this terminology. McDowell has not yet developed his arguments in the literature but he has been kind enough to provide me with unpublished material concerning his ideas. I agree that there is some degree of doubt with regard to the questioned homologies but I do not find compelling reasons to adopt McDowell's view. It does seem to me that in this case the "tradi-

tional" identifications of these bones are most compatible with the same named bones in *Captorhinus* (Fox and Bowman, 1966), a form that I hypothesize as a near relative of the turtles.

SQUAMOSAL

Figures 4, 7, 8, 53-65

DEVELOPMENT: The squamosal is a membrane bone that ossifies as a vertical plate lateral to the dorsal portion of the cartilage. The development of the antrum postoticum apparently occurs in stages later than the ones reported in the literature and a study of this structure might be useful.

CONTACTS: In all turtles the squamosal is attached to the posterodorsal region of the quadrate in a fairly extensive and broadly overlapping suture. In all turtles except *Dermochelys* the squamosal also reaches the processus paroccipitalis of the opisthotic posteromedially. The anterolateral corner of the squamosal contacts the quadratojugal except in those forms that lack or have reduced the quadratojugal (such as chelids and some emydids). The anterolateral corner may also contact the postorbital in forms with a relatively well-developed skull roof: chelydrids, most chelonoids, baenids, and some emydids. A parietal-squamosal contact exists in most chelonoids, some baenids, and most chelids (but not *Chelodina*). The chelid parietal-squamosal contact tends to be in the form of a bar of bone due to the extensive lateral or cheek emargination. In *Crossochelys* and an undescribed Miocene podocneme the squamosal contacts the supraoccipital (see Temporal Emargination for discussion).

STRUCTURES: The squamosal (fig. 4, 53) is a cone-shaped bone lying posterodorsally above the cavum tympani of the quadrate and participating in the formation of the antrum postoticum. The interior of the squamosal forms a considerable portion of the antrum postoticum, whereas the exterior surface is involved in muscular attachment.

The antrum postoticum is a cone-shaped cavity with its apex pointing posteriorly and its base opening anteriorly into the posterodorsal

region of the cavum tympani into which it grades. The incisura columellae auris is usually considered to mark the anteroventral limits of the antrum postoticum but there is no distinctive boundary between the cavum tympani (*sensu stricto*) and the antrum postoticum. The quadrate usually forms part of the base of the antrum, whereas the squamosal forms the upper area. In some forms, such as *Geochelone* (*sensu* Loveridge and Williams, 1957) the quadrate underlies almost all of the squamosal and the surface of the antrum consists mostly of quadrate.

The size of the antrum postoticum is somewhat variable. Romer (1956, p. 508) and Loveridge and Williams (1957, p. 472) stated that cheloniids lack an antrum postoticum but, although it is reduced and shallow in comparison with other turtles, it is not absent as in other reptiles. Most adult *Carettochelys*, however, have no trace of a concavity within the cavum tympani but in a juvenile (AMNH 85893) and an adult (AMNH 108910) there is a small but distinct antrum postoticum (I am grateful to S. B. McDowell for bringing this to my attention). Only *Proganochelys* definitely lacks an antrum postoticum. Testudinoids have a relatively large antrum, especially such forms as *Testudo* and *Geochelone*. The antrum in chelids is usually long and tubular, in *Chelus* it is unusual in that it extends medially for a considerable distance as a narrow tube. Pelomedusids tend to have a reduced antrum although it is not as small as in cheloniids.

The external surface of the squamosal serves as attachment sites for jaw muscles. M. adductor mandibulae fibers originate on the medial and dorsal surfaces, whereas the depressor mandibulae originates on the lateral and ventral surface (Schumacher, 1954, 1955a, 1955b). The development of a posteriorly directed spine or process in some forms (trionychids and some chelids) is apparently related to attachment sites for this musculature. The depressor mandibulae may attach in a distinct trough on the ventrolateral surface (e.g., *Chelodina*, *Caretta*) and what appear to be the limits of the muscle can be seen on the bone in some cases. A ridge (as in *Caretta*) may develop within the origin area

of the depressor mandibulae which apparently reflects the division of the muscle into two heads.

McDowell (1964) has used the name "supratemporal" for what I term here squamosal (see Quadratojugal for discussion).

POSTORBITAL

Figures 3, 4, 7, 8

DEVELOPMENT: The postorbital is a membrane bone that ossifies behind the orbit in a form very similar to its adult shape.

CONTACTS: The postorbital is one of the main components of the temporal arch (except in *Chelodina* and other forms lacking a temporal arch) and contacts the parietal posterodorsally, the frontal anterodorsally, and the jugal ventrally. A posteroventral contact with the quadratojugal exists in most turtles but is absent in *Podocnemis* (*sensu* Baur, 1890) due to reduction of the postorbital, in trionychids due to extreme development of temporal emargination and in those forms lacking a quadratojugal. The postorbital reaches the squamosal in chelonioids, chelydrids, *Platysternon*, and some emydids (in which the temporal emargination does not cause a separation). There may be a postorbital-prefrontal contact in some turtles (e.g., *Chelydra*), resulting in the exclusion of the frontal from the orbital margin. The postorbital of pleurodires has a ventrally directed process that, along with the jugal, reaches the palatine and pterygoid (see below).

STRUCTURES: As Siebenrock has remarked (1897), the postorbital has a greater size range than any other bone in the skull of turtles. In many chelonioids and chelydrids, particularly *Dermochelys* and *Platysternon*, the postorbital is relatively large and forms a major part of the temporal roof. Forms that have a greater degree of posterior temporal emargination tend to develop this at the expense of the postorbital so that the size of the bone decreases. It is particularly small in some trionychids, emydids, and testudinids. The postorbital of chelids is reduced because of lateral cheek emargination although it is somewhat larger in *Chelus* and *Pseudemydura*. *Podocnemis* (*sensu* Baur, 1890)

is unusual in having a well-developed dermal roof with a quite reduced postorbital. In some individuals of *Podocnemis expansa* the bone may be entirely lacking on the dorsal surface (Ruckes, 1937b; Ruckes did not state whether the ventral portion of the postorbital persists hidden from dorsal view). Some specimens of *Kinixys belliana* have been reported (Ruckes, 1937a; AMNH 10029) as lacking a postorbital apparently due to extreme development of the posterior temporal emargination (McDowell, 1964, commented that some reported absences of bones resulted from loss during preparation and that should be kept in mind here).

The postorbital forms the posterodorsal margin of the orbit and the posterodorsal wall of the fossa orbitalis. In most cryptodires this wall is not well developed and there is a large passage between the fossa orbitalis and the fossa temporalis inferior. Trionychids, however, tend to develop a wall in this area by enlarging portions of the maxilla, jugal, and postorbital. Pleurodires also tend to have a well-developed posterior wall for the fossa orbitalis but in this case the postorbital makes up the major part and reaches the pterygoid and palatine. It is likely that this ventral development of the postorbital in pleurodires is related to the bracing of the processus trochlearis pterygoidei (see Jugal for pleurodire modifications of the postorbital wall).

Zangerl (1948b) has set up morphotypes (see Temporal Emargination) for the temporal region of the chelonian skull that summarize the size variations of the postorbital bone.

TEMPORAL EMARGINATION

Figures 7, 8

The variable development of the dermal skull roof in turtles has been known for some time. Gaupp (1895), van Bemmelen (1896), and Siebenrock (1897) discussed the emargination of the chelonian temporal roof. Zdansky (1925) and Kilius (1957) are the most extensive works on this part of the skull, and along with Zangerl (1948b) form the basis of my review. Kilius (1957) groups the families of turtles by the degree of emargination, using the number

and types of bones exposed along the edge of the emargination to determine the extent of temporal reduction. Zangerl uses the emargination as an example of morphologic methodology and does not systematically cover the turtle groups, whereas Kilius does attempt to describe the skull roof condition in all turtles.

In general, the emargination patterns are of two sorts; termed by Kilius caudal reduction, which develops posterodorsally, and lateral reduction, which develops ventrolaterally in the cheek region. However, there is one case of apparently "true" temporal fenestration as seen in other reptile groups, and this is *Crossochelys*, an Eocene meiolaniid (Simpson, 1938). Simpson (1938, pp. 236-237) commented on the possible origin of the fenestra. "The temporal fenestra of *Crossochelys* has the superficial aspect of the normal supratemporal opening of other reptiles (except Anapsida), that is, of the single parapsidan opening of the upper of the two diapsidan openings, but this is certainly not a homology. The posttemporal bar in *Crossochelys* is not, as in other reptiles, formed by dorsal elements, usually parietal, squamosal, or both, but by the supraoccipital and the squamosal. Evidently it has arisen from a form with a superoposterior notch and a supraoccipital produced into a dorsoposterior spine, a normal and widespread chelonian condition, by the lateral expansion of the posterior part of the supraoccipital and the medial expansion of the posterior part of the squamosal. These processes have met, cutting off the anterior part of the notch and leaving it as an enclosed fenestra which thus is not a perforation in origin and has nothing to do with the normal reptilian supratemporal opening. In *Niolamia* further expansion of the surrounding elements has closed the fenestra and produced a secondarily complete roof." And in a footnote (*ibid.*): "As elsewhere noted, it is possible that the opening is a juvenile character in *Crossochelys* and that the adult had a complete roof, but even in this case the evidence as to the historical origin of the roof is valid."

A discussion of temporal emargination is hampered by two factors. First, the adaptations and biological roles of the temporal roof are

not well understood. Classically, the literature generally presents the idea of a conflict between more bone for protection and less bone for muscle "expansion." Turtles lacking emargination do tend to have poorly developed neck retractile mechanisms but this is not always the case (most chelids have extensive emargination but little shell protection for the head). Furthermore, the function of temporal fenestration in general has recently been reexamined by Frazetta (1968) and he suggested that traditional "muscle expansion" ideas are wrong. In any case, turtle jaw muscle studies (Schumacher, 1954, 1955a, 1955b) do not show any correlation between basic muscle morphology and degree of temporal emargination. Furthermore, examination of the known diversity of Recent and fossil turtle groups shows that many family level taxa include emarginated as well as well-roofed forms.

The second difficulty involves the determination of landmarks for comparative purposes. The relative degree of emargination can be indicated by reference to other skull structures, for example, the foramen stapedio-temporale, by citing the absence of bone contacts, or by citing the bones exposed along the temporal margin. However, the variable size of roofing bones may lead to ambiguities when these methods are used. For example, the Protostegidae are reported (Wieland, 1900, p. 241; Zangerl, 1953, fig. 32) to have a parietal-squamosal contact, a condition usually considered characteristic of a well-roofed skull, but the contact is extremely narrow and a relatively deep emargination is present when compared with *Dermochelys* or *Platysternon*. Therefore, although temporal emargination has been used extensively in turtle systematics some understanding of its limits are necessary.

The following discussion attempts to describe the range of variation present in family-level taxa but does not attempt to indicate the temporal condition in all known turtles. Because Kilius' work (1957) is the most systematic to date, I follow, in general, his method of description, that is, indicating the bones exposed along the temporal emargination. Also, I

add a more subjective statement about the relative degree of emargination.

The condition of the skull roof in the Triassic turtles would be interesting and even useful if it were known. The only first-hand description is by Jaekel (1916) and he expressed considerable doubt about the position of sutures. Later interpretations (Romer, 1956, 1966) differ a great deal from one another and do not appear to be based on reexamination of the specimens. There seems to be some posterodorsal emargination in Jaekel's reconstruction of a crushed specimen but the well-preserved Stuttgart specimens have not been figured in dorsal view so the condition is unsubstantiated. Cheek emargination (lateral reduction of Kilius) is completely absent in both Jaekel's (1916) and Parsons and Williams' (1961) illustrations.

The baenoids are relatively consistent in maintaining a moderate degree of emargination except in the youngest forms (Eocene). *Glyptops* (Jurassic) is not well known in this region, but is certainly no more emarginate than *Trinitichelys* and possibly less. *Trinitichelys* (Early Cretaceous) has a minute squamosal-parietal contact and a partial cheek emargination. The Late Cretaceous baenids (with the probable exception of *Palatobaena*) have more extensive posterodorsal emargination and the postorbital is well exposed in the temporal margin. Cheek emargination is not extensive in any known baenoid.

Among Jurassic turtles a moderate amount of posterodorsal emargination is usually present. In *Plesiochelys* the area is not completely known but appears to have a small part of the postorbital entering the temporal margin and the foramen stapedio-temporale is exposed in dorsal view (Gaffney, 1975b).

Although the living chelonoids have the best-developed temporal roof of living turtles, fossil chelonoids tend to be more emarginate. Toxochelyid emargination seems to be variable, *Erquelinnesia* (Eocene) seems to have a well-developed roof but the sutures are in doubt, whereas *Toxochelys* is more emarginate and has an unusual process of the parietal that prevents more extensive exposure of the postorbital.

Protostegids also have a moderate emargination but in this group a process of the squamosal completely prevents postorbital exposure. Living cheloniids and *Dermochelys* are the traditional examples of primitively well-roofed turtles but some authors (i.e., Zdansky, 1925) consider this condition secondarily derived from a more emarginate ancestor. Comparatively well-developed emarginations exposing the postorbital in the Cretaceous cheloniids, *Corsochelys* (Zangerl, 1960) and *Desmatochelys* (Zangerl and Sloan, 1960) seem to support this condition.

In the Testudinoidea, the chelydrids (including *Platysternon*) have variable emargination with parietal, squamosal, and postorbital exposed along the posterior border. *Platysternon* has a more extensive temporal covering, however, than does *Chelydra*. In the testudinids the emargination reaches the quadratojugal and that bone as well as the parietal, squamosal, and postorbital form the margin of the temporal emargination. The Emydidae show considerable variation in this area with all living forms possessing some degree of skull roof reduction. The least emarginate condition (again using Kilius' criteria) in Emydidae has the parietal, squamosal, and postorbital exposed (as in *Clemmys* and *Chrysemys*); further emargination results in the exposure of the quadratojugal (*Batagur*, for example); and the jugal enters the temporal margin in still more emarginate forms (*Geoclemys*). The temporal arch is completely lost in *Hieremys*, some species of *Terrapene* and some species of *Geoemyda* (see Quadratojugal) with consequent absence of the quadratojugal. Some emydids (such as *Geoemyda trijuga*, and *Nicoria*) may also have the quadrate exposed due to separation along the quadratojugal-squamosal suture. An undescribed early Tertiary testudinoid (PU 14671 and 17794, identified as *Ptychogaster* by Baird and Wood, personal commun.), however, has a greatly expanded caplike skull roof and is an important exception to the usual emarginated condition. The extinct meiolaniids also are well known for a well-developed skull roof (see above) and the formation of this roof by a squamosal-supraoccipital

contact (in the one form with sutures) increases the likelihood of secondary derivation.

Within the Trionychoidea (as here construed including Kinosternidae and Dermatemydidae, Gaffney, 1975d) *Dermatemys* has the squamosal, quadratojugal, postorbital, and parietal exposed in the posterodorsal region similar in extent to batagurine emydids. Kinosternids usually have the same bones plus the jugal exposed in a posterodorsal emargination that is greater than in *Dermatemys*; for example, in *Claudius* there is only a slender bar between the orbit and the emarginated fossa temporalis. Trionychids have very extensive emarginations and, in most genera, the parietal, jugal, quadratojugal, and squamosal form the margin. In *Trionyx* the postorbital may also be exposed. *Carettochelys* has parietal, postorbital, quadratojugal, and squamosal exposed and also the quadrate. Most trionychoids have only a slight development of cheek emargination.

The two families of living pleurodires have a quite divergent temporal region. *Pelusios* and *Pelomedusa* have the parietal, postorbital, squamosal, and quadratojugal exposed, whereas *Peltocephalus*, *Erymnochelys*, and *Podocnemis* have a more complete temporal roof limited by the squamosal, quadratojugal and parietal. The postorbital of *Podocnemis* (*sensu* Baur, 1890) is greatly reduced and the quadratojugal forms much of the temporal roof in contrast to most cryptodires and other pelomedusids. An undescribed podocnemine from the Miocene of Africa (Bramble, in prep.) has a meiolaniid-like roof in which an enlarged squamosal contacts the supraoccipital to form an extensive covering on the back of the skull.

Chelids possess extensive lateral emargination, lack the quadratojugal, and usually have the quadrate, squamosal, parietal, postorbital, and jugal forming the edge of the emargination. In *Chelodina* the squamosal-parietal contact is lost and there is no temporal arch. A parietal-quadrate contact prevents the emargination from reaching the squamosal in the relatively well-roofed *Pseudemys*. The postorbital is comparatively large in *Chelus* and prevents ex-

posure of the jugal along the emargination. *Batrachemys*, *Hydraspis*, *Chelus*, and *Phrynops* have well-developed emargination with only a

narrow parietal-squamosal bar remaining, while *Elseya*, *Emydura*, *Platemys*, and *Pseudemydura* have a more extensive temporal roof.

PALATAL ELEMENTS

PREMAXILLA

Figures 2, 9, 53-83

DEVELOPMENT: The premaxilla is a membrane bone that lies beneath the nasal capsule. As de Beer remarked (1937, p. 259) there is no

embryological suggestion of a premaxillary process separating the narial openings as in other reptiles and some fossil turtles. An egg tooth is absent (*ibid*).

CONTACTS: Laterally, the premaxilla con-

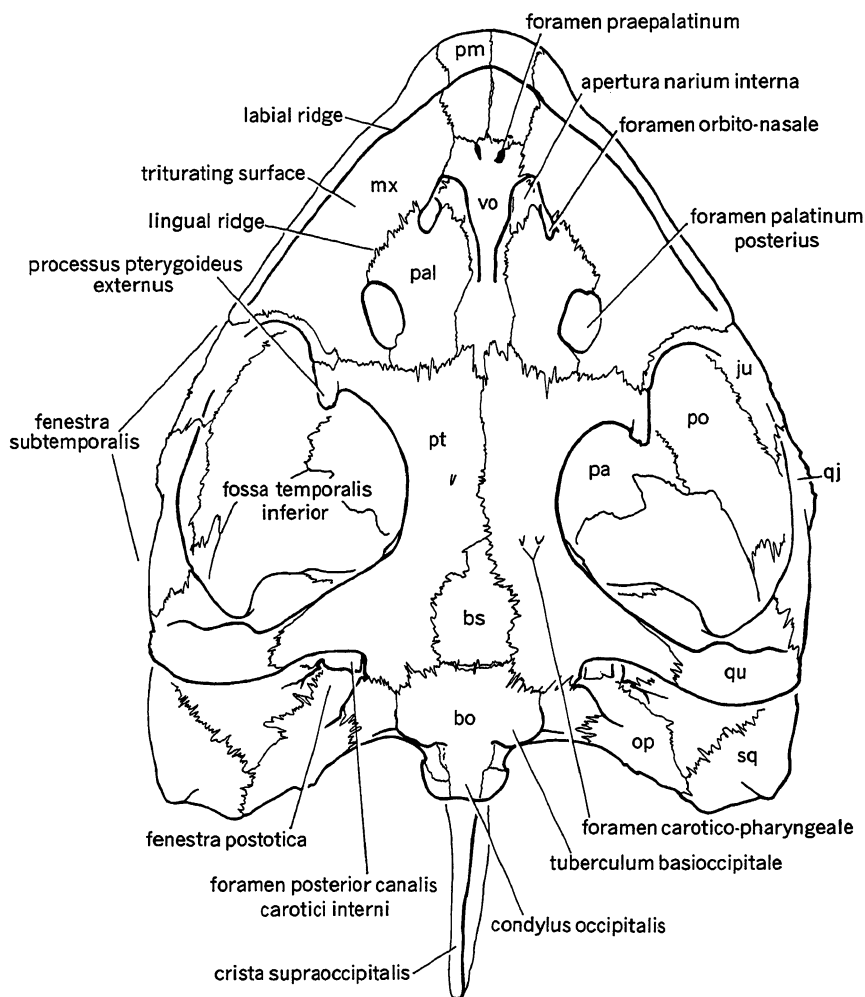


FIG. 9. Palatal view of *Chelydra serpentina* (AMNH 5305), Chelydridae, no data, showing major structures (from Gaffney, 1972b). See also figure 207.

tacts the maxilla in a broad suture and posteriorly, the premaxilla contacts the vomer. The premaxilla is paired in most turtles and meets its mate medially for its whole length. In many living pelomedusids the vomer is lacking and the premaxillae either border a single, large apertura narium interna or are bordered posteriorly by the maxillae.

Trionychids usually have no vomer-premaxilla contact due to the reduction of the ventral portion of the vomer and/or the development of the foramen intermaxillaris, an opening in the palate anterior to (or, in *Carettochelys*, confluent with) the apertura narium interna. Cheloniids may not have a vomer-premaxilla contact in ventral view (but retained dorsally in the floor of the fossa nasalis) due to medial expansion of the palatine process of the maxillae.

STRUCTURES: The premaxilla is usually a small, roughly triangular element, narrowest posteriorly and situated at the anterior edge of the skull directly beneath the apertura narium externa. Although the premaxilla is usually paired, in *Chelus* and trionychids it is fused, at least in most adults. There is not a great deal of size variation in the premaxilla but it is relatively small in many trionychids and may be absent (some specimens of *Cycloderma frenatum*, Loveridge and Williams, 1957, p. 462).

The dorsal surface of the premaxilla forms the floor of the fossa nasalis and the anterior edge of the bone is usually the ventral margin of the apertura narium externa. In most reptiles the apertura narium externa is divided by a median dorsal process of the premaxilla (or premaxillae) into two openings. A single apertura is characteristic of turtles but there are exceptions. In the Triassic turtle *Proganochelys* the dorsal processes of the premaxillae extend up to insert between the nasals (Parsons and Williams, 1961, p. 91) in a manner similar to other reptiles. Nopsca (1923) has described paired nares in *Kallokibotion* (Late Cretaceous), a baenoid cryptodire; and meiolaniids (Anderson, 1925) also have an internasal septum. In the case of the last two forms, however, sutures are lacking or are in doubt and it is not known what elements divide the nares and, therefore, it cannot be determined if

the condition is due to dorsal premaxillary processes.

The premaxilla forms the anteromedial portion of the cranial triturating surface (see Maxilla, for discussion) and usually carries a continuation of the labial ridge. In the midline (where the two premaxillae meet) a notch (*Dermochelys*) or a toothlike hook (*Erymnochelys*, *Macrolemys*, *Platysternon*) may be present. Often the triturating surface has a variably developed median concavity or posteriorly directed trough behind the labial ridge. Transverse ridges (or commissural ridges, *vide* McDowell) on the maxilla and/or premaxilla may parallel the maxilla-premaxilla suture (as discussed under Maxilla). If the ridges and concavity are present (as in most species of *Geochelone*, *sensu* Loveridge and Williams, 1957; *Batagur*, and *Dermatemys*) then this premaxillary area is quite distinct from the rest of the triturating surface.

The premaxilla usually is involved in the formation of the foramen praepalatinum, a small opening extending between the palate and the floor of the fossa nasalis. The foramen praepalatinum transmits the anterior nasal artery from the palate to the nasal tissue (Seydel, 1896; Albrecht, 1967, p. 94). The foramen is usually formed along the vomer-premaxilla suture but it may be formed entirely by either bone. The foramen praepalatinum is absent in some turtles, such as cheloniids. In the trionychids and carettochelyids the region behind the premaxillae is occupied by a variably developed opening, the foramen intermaxillaris. This structure may be small (e.g., *Cycloderma frenatum*) or extremely large and include the apertura narium interna (e.g., *Carettochelys*). The foramen praepalatinum is absent in trionychids and carettochelyids presumably in relation to the development of the foramen intermaxillaris.

A few small alveoli are reported on the premaxilla of *Proganochelys* ("*Triassochelys*," Jaekel, 1916) but no other turtle is known to have any evidence of teeth.

MAXILLA

Figures 1, 30-33, 53-83

DEVELOPMENT: The maxilla is a membrane bone that ossifies along the anterolateral edge

of the palate. Three regions are recognized by Kunkel (1912, p. 749): the processus palatinus, lying in the same plane as the palatine bones; the processus alveolaris, extending ventrally as the labial ridge; and the processus praefrontalis, embracing the posterior portion of the olfactory capsule.

CONTACTS: The most common contacts of the maxilla are as follows: premaxilla anteromedially, vomer and palatine medially, pterygoid posteriorly, and jugal posterolaterally. In most chelids the maxilla reaches the nasal, whereas in some species of *Trionyx* it reaches the frontal. The maxilla in pelomedusids and cheloniids usually does not meet the pterygoid due to contact of the jugal and palatine. In some trionychids (e.g., *Trionyx*) the maxillae may meet anteriorly along the ventral edge of the apertura narium externa and medially along the roof of the palate. The maxillae may meet medially in some living cheloniids (e.g., *Caretta*) between the premaxillae and vomer but this seems somewhat subject to individual variation.

STRUCTURES: "The maxilla is a large element with two main portions, a vertical part and a horizontal part. The former forms the surface of the face anterior and ventral to the orbit" (Parsons and Williams, 1961, p. 54). The horizontal or palatine plate forms the floor of the fossa orbitalis and bears part of the horny beak (rhamphotheca) on its ventral surface. Siebenrock (1897) divides the vertical plate into two sections, a more dorsal prefrontal process and a more ventral alveolar process.

The alveolar process of the maxilla is usually a thin, sharp blade enclosed on both sides by the horny beak. The horny material usually follows the contours of the bone and rarely are there any major structures present in one and not in the other, although serrations, small ridges and tubercles may occur in the rhamphotheca and not on the bone (e.g., *Macrolemys*, *Caretta*). The alveolar plate may be deep and sharp, as in *Geochelone* (*sensu* Loveridge and Williams, 1957), or shallow as in *Chelus* and most chelids. Some forms may have a serrated ventral margin (e.g., *Geochelone sulcata*) or a notch (*Dermochelys*). The

alveolar plate is reported to bear a few small alveoli in *Proganochelys* (Jaekel, 1916) but there is no evidence of teeth in other turtles.

The prefrontal process of the maxilla is a dorsal continuation of the anterior part of the vertical alveolar plate. Anteriorly it forms the lateral margin of the apertura narium externa and medially the lateral wall of the fossa nasalis. The posterior edge of the prefrontal process lies along the anterior margin of the fossa orbitalis and has a long, curved suture with the prefrontal.

The palatine process is a horizontal plate that extends medially, forms the floor of the fossa orbitalis, and is covered on its ventral surface by the horny beak or rhamphotheca. Rarely (as in *Chelus*, *Dermochelys*, and *Glyptops*) the palatine process may be narrow and nearly absent, but usually it is more or less developed into a crushing or triturating surface. Because it is supposedly this area that bears teeth in most other reptiles the term alveolar surface has also been used for it (see discussion below).

A series of foramina and canals occur in the maxilla of most turtles. The main canal is roughly Y-shaped and is termed the canalis alveolaris superior. The lateral section of the canalis runs posterolaterally within the maxilla from the anterior part of the maxilla and roughly parallels the labial ridge. A branch runs posteromedially off the main part of the canal and ends at the foramen alveolare superius. This branch usually comes off the anterior section of the canalis alveolaris superior. The canalis alveolaris superior and the foramen alveolare superius contain the superior alveolar artery (arteria alveolaris superior) and its branches which supply blood to the maxilla, the epithelium around the maxilla and part of the nasal capsule tissue (Albrecht, 1967, p. 91). The foramen alveolare superius usually occurs along the ventrolateral edge of the foramen orbito-nasale but within the region of the fossa nasalis.

Another canal branches off the posterior portion of the canalis alveolaris superior, and this branch is the canalis infraorbitalis. The canalis infraorbitalis extends posteriorly in the maxilla

to open into the floor of the fossa orbitalis via the foramen supramaxillare. The canalis infraorbitalis and the foramen supramaxillare usually contain the supramaxillary artery (arteria supramaxillaris), although Albrecht (1976) was unable to find the artery in a specimen of *Trionyx cartilagineus*. "Its function probably is that of supplying the branches of the trigeminal nerve within the canalis infraorbitalis and canalis alveolaris superior" (Albrecht, 1967, p. 91). Although *Podocnemis* has a foramen supramaxillare, most pleurodires do not (Albrecht, 1976).

THE FEEDING SURFACES OF TURTLES: The morphology of the areas covered by the horny beak in turtles is of considerable usefulness in systematic work but no extensive comparative study has been done. Although I am not attempting to fill this gap, I present the following brief review to indicate the degree of differences and types of structures known.

It is difficult to define precisely the area involved, and the terms used in the literature are not completely satisfactory. The region can be more specifically characterized as the bony area covered by the horny beak, or rhamphotheca. The terms triturating and alveolar have been used but the former means crushing and the latter refers to tooth bearing—neither of which characterizes the turtle feeding surface in many cases. I do prefer triturating surface and use it here in an expanded sense to mean the area covered by the rhamphotheca. Various names have appeared for structures on the triturating surface, and I have contributed to the confusion in this area. Many authors use the term tomial ridge for the most lateral ridge (the ventral edge of the alveolar process) but in Gaffney (1972b, figs. 2, 14, 16) the tomial ridge is the medial ridge. It seems better to use the positional terms labial and lingual for the most lateral and most medial ridges, respectively, and abandon the term tomial (which means cutting or slicing) ridge. Most turtles have a sharp, well-defined labial ridge and a lower, sometimes absent, lingual ridge but in many cases additional ridges or depressions occur on the triturating surface and in this case they are, by definition, between the labial and

lingual ridges. Although the labial ridge appears to be homologous in all known turtles, the lingual ridge is more doubtful, and in any case, I use these as positional terms and do not necessarily imply homology.

According to the figures in Jaekel (1916, fig. 47) and Romer (1966, fig. 166), the triturating surface of the Triassic turtle, *Proganochelys*, is relatively narrow (although the palatine process is apparently not so narrow as it is in *Chelus* and *Dermochelys*), the labial ridge is well developed and high, and the lingual ridge is low or absent. The triturating surface may be slightly concave ventrally. This condition appears to be satisfactory as the primitive condition for all turtles. Most post-Triassic turtles (the Casichelydia of Gaffney, 1975d) have a similar morphology but with a greater medial expansion of the triturating surface, either by expansion of the palatine process of the maxilla or by incorporation of the palatine bone into the triturating area.

Living pelomedusids tend to be conservative with a few low ridges on the triturating surface in some species of *Podocnemis* (see Williams, 1954a). Some fossil pelomedusids have developed an incipient secondary palate (as in *Shweboemys*, Wood, 1970, fig. 1), in which the labial and lingual ridges are low and the palatine process of the maxilla (along with the palatines) is expanded medially and nearly meet along the midline. The Late Cretaceous pleurodire *Bothremys* (Gaffney and Zangerl, 1968) has one of the most unusual triturating surfaces of any turtle. In this form the maxilla, palatine, and especially the jugal form a large pit, opening ventrally, in each cheek that matches a similar pit in the lower jaw (facing upward) resulting in a pair of spherical cavities formed when the jaws are shut. It seems likely that these structures were covered by the horny rhamphotheca but their function is unknown. Chelids vary from a high labial ridge, low or absent lingual ridge, and moderately expanded triturating surface in forms such as *Emydura macquarrii* to a condition with reduced triturating area and low ridges. *Chelus* has a quite narrow palatine process and a narrow triturating area, the labial ridge is low and the lingual

ridge is low and on the palatine bone. Although this position of the lingual ridge seems anomalous, comparison with other turtles suggests an explanation. In most turtles the palatine bone meets the palatine process of the maxilla in the area between the foramen palatinum posterius and the apertura narium interna. In this area the palatine usually makes up part of the triturating surface, is covered with rhamphotheca, and may form part of the lingual ridge. In *Chelus* the foramen palatinum posterius and the apertura narium interna are reduced in size and widely separated resulting in a considerable expansion of the lingual ridge area formed by the palatine.

Baenoids have a considerable amount of variation in triturating surfaces. In *Glyptops plicatulus* the labial ridge is high and thin, the lingual ridge is quite low and nearly absent, and the triturating surface is very narrow, much as in *Chelus*. Other baenoids have a well-developed medial expansion of the triturating surface with an incipient secondary palate in *Eubaena* and laterally expanded crushing surfaces in *Palatobaena*.

Many fossil and recent cheloniids have a well-developed secondary palate differing from the previously mentioned incipient secondary palates by the incorporation of a wide vomer plate into the midline of the palate thereby forming a solid roof. Some toxochelyids also have secondary palates. Zangerl (1953, pp. 148-153) described the palates in three Late Cretaceous genera: *Toxochelys*, with a primitive, primary palate; *Ctenochelys*, similar to *Eubaena* (previously mentioned) with an incipient secondary palate; and *Osteopygis*, with an extraordinarily extensive secondary palate. A better known near relative of *Osteopygis* is the Eocene *Erquelinnesia* (Zangerl, 1971) a form that has the most extensive secondary palate known in turtles. Zangerl (1971, p. 13) compared the palates of a series of chelonoids, including *Erquelinnesia*:

"In *Chelydra* and *Toxochelys* the choanal openings communicate directly with the nasal chamber. This is also true in *Ctenochelys*, but here we see an incipient stage in the series leading to the secondary palate: the anterolateral wings of the vomer are

rugose and thick, the triturating surfaces are relatively broader due to medial extension of the maxillae, augmented by ventromedial expansion of the palatines. The next stage is represented by *Eretmochelys* in which the vomer forms a short, sagittal pillar separating very short nasal passages between the nasal chamber and the choanal openings. In *Chelonia* the vomer pillar is considerably longer (as are the nasal passages) and it ends, as in *Eretmochelys*, at the choanal openings. *Caretta* resembles *Chelonia*, but here the edge of the choana lies some distance behind the posterior termination of the vomer pillar. In *Erquelinnesia* the vomer pillar is much elongated and the undershelfing of the nasal passages extends considerably beyond the posterior end of the pillar, back to the region of the basisphe-noid. In the modern cheloniid genera illustrated in figure 8, although they have secondary palates, the position of the vomer and palatines with regard to the skull as a whole is much the same as in forms with primary palates. In *Erquelinnesia*, however, both bones are posteriorly displaced, and the premaxilla extends much farther backward than in the compared forms."

Dermochelys has a primary palate and a relatively narrow triturating surface but the Eocene dermochelyid *Eosphargis breineri* (Nielsen, 1959) appears to have wider palatine processes of the maxilla and a more posterior position of the apertura narium interna. The presumed protostegid *Rhinochelys* (Collins, 1970) has a "normal" *Chelydra*-like palate with high labial and low lingual ridges but *Archelon ischyros* (Wieland, 1900) seems to have a somewhat unusual palatal configuration with a narrow, birdlike snout, enormous hooked premaxillae and, apparently a reduced palatine process of the maxilla.

The emydids also have a number of species with secondary palates or enlarged triturating surfaces. McDowell (1964) has argued that a particular triturating surface morphology is primitive for the Emydidae. He described the pattern as follows: "Both *Chrysemys alabamensis* and *Hardella* have very broad triturating surfaces, with a pair of longitudinal middle ridges on both the upper and lower triturating surfaces. In both turtles the middle ridge of the upper surface ends anteriorly in a strong cusp close to the common meeting point of the vomer, premaxillary, and maxillary, and in

both turtles a crest runs forward from this cusp close to the maxillo-premaxillary suture to connect with the "tooth" on the tomium flanking the median premaxillary notch; in both turtles the cusp is joined by a short commissural ridge to a median keel on the vomerine contribution to the triturating surface. In both the American and the Indian turtle, the middle crest of the lower triturating surface ends anteriorly in a cusp that bites posterolateral to the cusp of the upper surface; and in both turtles, the cusp on the lower surface is connected by a commissural ridge to a median keel that runs forward to the strong terminal hook of the dentary" (1964, p. 248).

Other emydids (e.g., *Malaclemys terrapin* and *Chinemys reevesi*) may have a secondary palate but lack the ridges or cusps on the ventral surface of the palatine process, while others may have additional ridges (e.g., *Batagur batagur*). A possibly significant difference between the secondary palates of emydine and batagurine turtles (*sensu* McDowell, 1964) is the presence of the palatine in the triturating surface of most emydines and its absence in most batagurines. Other emydids (such as *Deirochelys reticularia*) have relatively narrow triturating surfaces. McDowell (1964) has developed a hypothesis that, for emydids, the narrow condition is derived and the broad condition is primitive. There is considerable evidence of rather substantial sexual dimorphism in the triturating surfaces of some emydids, particularly *Malaclemys* and *Graptemys* (see Carr, 1952; Cagle, 1952; Ernst and Barbour, 1972). In these forms the females have greatly expanded maxillary and palatine contributions to enlarged triturating surfaces while the males have smaller surfaces (and skulls in general) with lesser development of maxilla and palatine.

Testudinids are relatively conservative in palatal morphology. The labial ridge is usually high and thin, the lingual ridge low and blunt and the triturating surface narrow with no approach to a secondary palate. An accessory ridge, similar to that described by McDowell (1964) for emydids, may run between the labial and lingual ridges to a commissural ridge (in McDowell's terminology) lying along the pre-

maxilla-maxilla suture (e.g., *Geochelone pardalis*) or the triturating surfaces may be smooth (e.g., *Kinixys belliana*).

The living chelydrids *Platysternon*, *Chelydra* and *Macrolemys* have somewhat similar triturating surfaces with a primary palate, a high labial ridge and low or absent lingual ridge, and an unexpanded palatine process of the maxilla. A symphyseal hook tends to be present although it is best seen in *Macrolemys* (see Premaxilla). A Paleocene chelydrid, *Protochelydra* (Erickson, 1973), however, has relatively broad triturating surfaces but no secondary palate.

Kinosternids tend to develop secondary palates (as in *Staurotypus*, fig. 167, and the most extreme condition seen in *Xenochelys formosa*, fig. 169; Williams, 1952b). *Dermatemys* (fig. 172) and its fossil relatives, *Adocus* (fig. 171; Late Cretaceous) and *Baptemys* (Eocene; these genera are badly in need of revision) have a somewhat distinctive triturating surface pattern. All of these forms have a moderately developed secondary palate, high labial and low lingual ridges, and a strong ridge roughly paralleling the premaxilla-maxilla suture. This last ridge is at right angles to the labial and lingual ridges and about 45 degrees from the midline and appears to be comparable to the "commissural ridge" discussed by McDowell (see above).

Trionychids usually have a blunt but high labial ridge but it may be very low as in *Chitra* and *Pelochelys*. The lingual ridge is low or absent and the palatine process of the maxilla can be relatively narrow (as in *Carettochelys*) or expanded into partial or complete secondary palates (e.g., *Pelochelys*). Dalrymple (1977) described considerable variation in the triturating surfaces of *Trionyx* that appears to be related to age and diet rather than sexual dimorphism as suggested earlier (Stejneger, 1944; Carr, 1952).

VOMER Figures 53-83

DEVELOPMENT: The vomer (prevomer of DeBeer, 1937) in *Emys* arises from "a pair of thin lamellae set at an angle to each other so

that they fit about the ventral edge of the septum interorbitale between the posterior opening of the ductus naso-pharyngeus behind and the cartilago paraseptalis in front" (Kunkel, 1912, p. 753). Later in development the two centers fuse into a single median troughlike element.

CONTACTS: The usual contacts of the vomer are as follows: Premaxilla anteriorly, maxilla anteroventrolaterally, prefrontal anterodorsally (except in pleurodires), palatine laterally, and pterygoid posteriorly. There are exceptions to all of these but the maxilla, which appears to have the most consistent contact with the vomer. The premaxilla contact is lost in trionychids and *Carettochelys* due to the development of the foramen intermaxillaris. Some chelids (e.g., *Platemys*, *Phrynops*, *Hydromedusa*) and cheloniids (*Caretta*) have maxillae that meet in the midline and prevent a vomer-premaxilla contact on the ventral surface but in all specimens that I have seen the vomer and premaxilla meet on the dorsal surface, that is, in the floor of the fossa nasalis (I would not be surprised to see this contact lost in some specimens). The palatine contact may be lacking (e.g., *Hydromedusa* and *Chelus*).

The prefrontal-vomer contact is absent in all pleurodires and some trionychids (*Chitra*, *Cycloderma* and some species of *Cyclanorbis*, Loveridge and Williams, 1957) but it occurs in all other cryptodires. Trionychids and *Carettochelys* are also unusual in having no vomer-ptyergoid contact.

A vomer-basisphenoid contact can be seen on the dorsal surface of the palate in some species of *Geochelone* (e.g., *G. elephantopus*) and, according to Siebenrock (1897), in *Pelochelys* (I have only been able to examine intact skulls of *Pelochelys*).

The vomer is absent in many living pelomedusids and some trionychids (most species of *Cycloderma*, Loveridge and Williams, 1957). According to Mittermeier and Wilson (1974) previous reports of a vomer occurring only in *Podocnemis vogli* (Williams, 1954a; and earlier references) are incorrect and they report a small but distinct vomer in most specimens of *Podocnemis erythrocephala*, *P. uni-*

filis, and *P. lewyana*, as well as *P. vogli* (this species group they informally term the "vomarine group").

STRUCTURES: The vomer (fig. 104) is an unpaired, elongate bone lying in the midline of the palate between the paired apertura narium interna. In most turtles the bone is roughly dumbbell-shaped with the anterior and posterior portions expanded and a narrow connecting bar separating the two apertura narium externa on each side. The anterior expansion is usually sutured to the premaxilla and the paired foramen praepalatium usually occurs in the suture or within the vomer or premaxilla (see Premaxilla, for discussion of the foramen praepalatium). The maxilla contacts the anterolateral portion of this expansion and the posterior edge of the vomer and maxilla (together with the palatine posterolaterally) usually form the margin of the apertura narium interna. Some types of secondary palates (particularly those seen in cheloniids, emydids, and kinosternids; see Maxilla) involve an expansion of this area of the vomer into a horizontal plate that is incorporated into the triturating surface and covered by the horny rhamphotheca. This reaches its most extreme development in *Erquelinnesia* (Eocene), a toxochelyid that has an extensive secondary palate with the horizontal plate of the vomer running posteriorly for a considerable distance and with the more dorsal portion of the vomer forming a septum (vomarine pillar) between the two nasal passages (Zangerl, 1971).

The anterodorsal area of the vomer participates in forming part of the floor of the fossa nasalis and usually has a median groove extending posteriorly, the sulcus vomeri, which supports the cartilaginous septum nasalis (Soliman, 1964, figs. 12, 23). Some cryptodires have a pair of anterolaterally directed processes on either side of the sulcus vomeri that articulate with the prefrontals. "In Trionychids the connection is mostly formed by ascending processes of the vomer meeting the prefrontals. In primitive turtles and in many modern forms (e.g., marine turtles), the prefrontal and vomer share about equally in this peculiar bony strut.

In testudinids the connection is almost entirely formed from the prefrontals'' (Loveridge and Williams, 1957, p. 419).

The posterior expansion of the vomer is well developed in testudinoids where this area is roughly T-shaped in cross section with the vertical plate at times reduced or absent. The horizontal plate forms part of the roof for the apertura narium interna and has a long lateral suture with each palatine.

PALATINE

Figures 9, 18, 19, 53-65

DEVELOPMENT: The palatine is a membrane bone that ossifies as a horizontal plate at the same level and between the pterygoid and maxilla.

CONTACTS: In most turtles the contacts of the palatine are as follows: vomer medially, prefrontal anteriorly, and jugal posterodorsolaterally. The prefrontal contact is lacking in trionychids (but present in *Carettochelys*) and pleurodires (with the exception of *Bothremys*; see Prefrontal for discussion). The jugal contact is absent in *Chelydra* (although just barely), many emydids and most testudinids. *Chelydra* lacks a parietal-palatine contact and most pleurodires (but not some chelids) lack a vomer-palatine contact. In trionychids and many pleurodires the palatines meet in a mid-line suture and in trionychids and pelomedusids the basisphenoid overlaps onto the dorsal surface of the palatine. Pleurodires have a postorbital-palatine contact in the posterior portion of the fossa orbitalis.

STRUCTURES: The palatine (fig. 103) occurs in the anterior portion of the palate and forms much of the palatal roof and part of the floor of the fossa orbitalis. The size of the palatine varies; it may be a broad sheet, as in *Chelus*, or it may be reduced to a thin, curved piece of bone, as in *Hydromedusa*. In most turtles the palatine consists of two areas, a more anterolateral plate that contacts the maxilla and participates in the formation of the triturating surface, and a more posteromedial plate that roofs the choana and is usually curved in cross

section. Many (but not all) forms with secondary palates have the triturating portion expanded (as in *Erquelinnesia* and Recent cheloniids) and displaced medially so that it lies above the choanal portion of the palatine with the choana between them. The resulting cross section is C-shaped and the vomer usually completes the nasal passage (or meatus choanae) medially. In other turtles, such as *Platysternon* and *Chelydra*, the palatine forms a well-defined lingual ridge but does not extend deeply into the triturating surface. In some forms (e.g., *Geochelone pardalis*) the palatine does not extend onto the triturating surface. *Dermochelys* is somewhat unusual in that the palatine process of the maxilla is greatly reduced and the palatine extends laterally to the edge of the labial ridge on the maxilla.

The palatine is involved in the formation of three major openings in the palate (fig. 9): the apertura narium interna, the foramen orbitonasale, and the foramen palatinum posterius. Participation in forming the apertura narium interna is variable. In most turtles the palatine is limited to the dorsolateral wall of the apertura but in forms with a secondary palate it may also form the ventral margin as well. In groups with a reduced or absent vomer (such as trionychids and pelomedusids) the palatine forms most or all of the dorsal margin of the apertura.

The foramen orbitonasale is the opening between the fossa nasalis and the fossa orbitalis and is usually situated in the posteroventrolateral region of the fossa nasalis. The foramen transmits the posterior nasal artery from the fossa orbitalis to the fossa nasalis (Albrecht, 1967) in *Chrysemys*, *Sternotherus*, and *Trionyx*. However, Bojanus (1819, fig. 147) and Albrecht (1967, p. 96) indicated that in *Kinosternon subrubrum* and *Emys orbicularis*, respectively, the superior alveolar and posterior nasal arteries (of Albrecht's terminology) arise as branches of the inframaxillary artery that runs from the palate dorsally through the foramen orbitonasale. It also contains a small nerve, a branch of the palatinus anterior (in Bojanus' terminology) and a branch of the maxillary (V₂) nerve (Bojanus, 1819, fig. 147).

In many turtles (e.g., cheloniids, chelydrids, kinosternids, some testudinids, some emydids) the foramen orbito-nasale is prominent and relatively large. Some testudinids (e.g., *Geocheilone*, sensu Loveridge and Williams, 1957) and some emydids (e.g., *Chinemys*, *Malayemys*), however, have a quite small and easily overlooked foramen orbito-nasale. Pleurodires lack a descending process of the prefrontal and, therefore, the foramen orbito-nasale is incompletely formed and confluent with the apertura narium interna and foramen interorbitale in the bony skull (I suspect that this is not the case in the adult chondrocranium). Trionychids also tend to lose the foramen as a discrete opening (especially *Carettochelys*) but it is retained in some (e.g., *Trionyx*, *Pelochelys*).

The foramen palatinum posterius is the opening between the palatal surface and the area just behind the fossa orbitalis (pleurodires) or the posteriormost limits of the fossa orbitalis (cryptodires). The foramen transmits the inframaxillary artery (arteria inframaxillaris) from the inside of the skull to the ventral surface of the palate. The foramen also contains a branch of the maxillary (V_2) nerve, the ramus palatinus anterior of Bojanus (1819, fig. 147). The palatine usually forms most of the foramen palatinum posterius and in some cases it forms all of the foramen (e.g., *Chelydra*). In most turtles the foramen palatinum posterius is small but it is relatively large in some turtles (e.g., *Deirochelys*) and completely absent in others, such as *Dermochelys* and recent cheloniids.

The position of the foramen palatinum posterius and the morphology of the dorsal surface of the palatine is of some interest in a comparison of cryptodires and pleurodires. Pleurodires

tend to develop a bony wall behind the fossa orbitalis that consists mainly of a dorsal palatine process with a lateral contribution from the jugal, a posterolateral contribution from the pterygoid and a dorsal contribution from the postorbital. The foramen palatinum posterius is always behind this wall, whereas in cryptodires the foramen is within the region of the fossa orbitalis. This condition is mostly due to the fact that in cryptodires this wall is absent and there is usually no definitive posterior limit to the fossa orbitalis. However, some cryptodires, such as *Trionyx*, may have a somewhat similar wall developed, but the palatine is not the major element in the wall and the foramen palatinum posterius is medial or anterior to the wall. The postorbital wall in pleurodires apparently has a bracing function for the pterygoid which in pleurodires bears the processus trochlearis pterygoidei, the major trochlea for the jaw musculature (see Pterygoid).

Dorsal processes of the palatine are also known in trionychids, kinosternids, *Carettochelys* and *Dermatemys*, but they are involved in the formation of the lateral walls of the braincase. The trionychids and kinosternids usually have a well-developed dorsal ridge on the palatine and it makes up the anteroventral portion of the braincase wall just anterior to the processus inferior parietalis. This ridge may be quite extensive and reach the skull roof, as in *Staurotypus*. Presumably, this process aids in bracing the palate against the braincase. The canalis nervi vidiani may penetrate the base of this process and emerge at the anterior edge of the braincase wall. A similar but usually less extensive process can be seen in some batagurines (e.g., *Batagur*).

PALATOQUADRATE ELEMENTS

QUADRATE

Figures 10-12, 16-19, 41, 47, 50, 51, 53-65, 85-102

DEVELOPMENT: The quadrate is a cartilage bone that ossifies in the posterior or quadrate portion of the palatoquadrate. In turtles the de-

veloping quadrate ossification obliterates much of the cranioquadrate space, the area between the palatoquadrate and the primary braincase, by forming extensive sutural contacts with the chondral braincase elements and the pterygoid.

CONTACTS: The squamosal has a broad, cir-

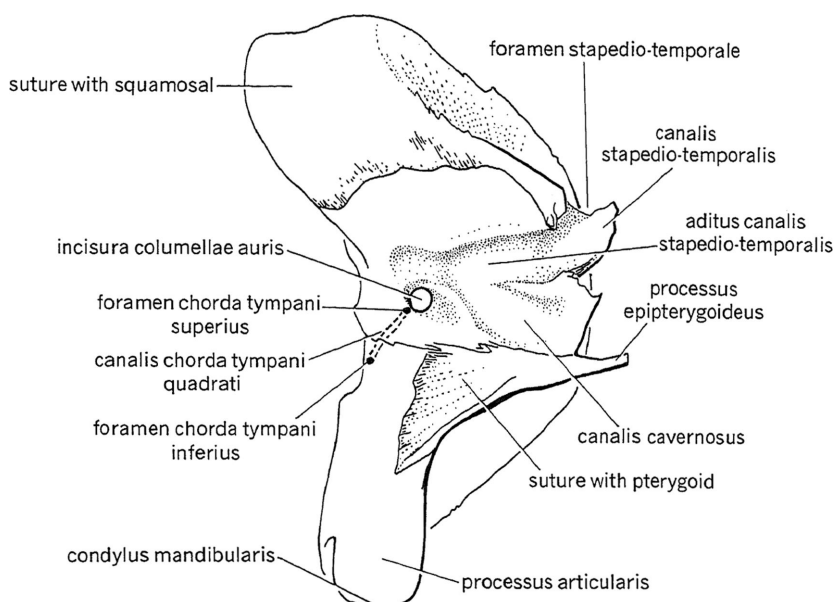


FIG. 10. Medial view of left quadrate in a cryptodire, *Chelydra serpentina* (AMNH 10786). For other figures of disarticulated quadrates see Siebenrock, 1897, figures 16 (*Chrysemys ornata*) and 17 (*Testudo graeca*); Kesteven, 1910, figures 31-35 (*Chelonia mydas*); and Ogushi, 1911, figures 20 and 24 (*Trionyx japonicus*). After Gaffney (1972b).

cular contact area along the dorsalmost portion of the quadrate. The medial section of the quadrate has broad contact areas with the opisthotic posteriorly and the prootic anteriorly. Ventral to these contacts the pterygoid is sutured to the quadrate. The extent of the pterygoid attachment is an important difference between cryptodires and pleurodires. Cryptodires usually have an extensive ventral pterygoid contact but pleurodires only have an anteromedial attachment to the pterygoid. Instead pleurodires have a process of the quadrate that extends medially to reach the basisphenoid and sometimes (in *Podocnemis*) the basioccipital. The quadratojugal contacts the anterolateral margin of the quadrate along the front edge of the cavum tympani except in those forms lacking a quadratojugal, such as chelids and some emydids. The parietal contacts the quadrate in *Testudo graeca* (Loveridge and Williams, 1957, fig. 21) just in front of the foramen stapedio-temporale and in some emydids (such as

Cyclemys dentata) above the foramen nervi trigemini. In most cryptodires the processus epipterygoideus of the quadrate reaches the epipterygoid but a small cartilaginous block (contained in the fossa cartilaginis epipterygoidei) may prevent actual contact. In *Terrapene* the quadrate reaches the supraoccipital.

STRUCTURES: The dorsal surface of the quadrate forms a portion of the floor of the fossa temporalis superior and part of the processus trochlearis oticum of cryptodires. In many cryptodires the quadrate forms the greater part of the processus trochlearis oticum, the rest being formed by the prootic (see Prootic, for full discussion of the processus trochlearis oticum). The foramen stapedio-temporale usually occurs in the suture between the quadrate and prootic (the foramen may be absent in some forms such as *Dermatemys*).

The anterior surface of the quadrate slopes ventrally to the condylus mandibularis (and forms the attachment area for portions of the

M. adductor mandibulae externus, Schumacher, 1954, 1955a, 1955b, 1973). Laterally, the quadrate consists of a more or less vertical sheet of bone separating the cavum tympani from the fossa temporalis inferior. Ventromedially, the quadrate tapers to a thin process, the processus epipterygoidei. This process usually overlaps the pterygoid laterally and extends beneath the foramen nervi trigemini (see Prootic). In cryptodires the epipterygoid usually meets or nearly meets this process but a block of cartilage (see Pterygoid, Development) a remnant of the embryonic palatoquadrate, may prevent contact. When this cartilage is lost in a fossil or dried Recent skull a depression, the fossa cartilaginis epipterygoidei, can be seen between the epipterygoid and the processus epipterygoidei of the quadrate. Baenids have apparently lost, or fused, the epipterygoid but the fossa cartilaginis epipterygoidei indicates the persistence of the cartilage remnant. Pleurodires, on the other hand, lack both an epipterygoid and a prominent fossa cartilaginis epipterygoidei. Pleurodires may be considered to have a greatly reduced, or absent, processus epipterygoidei and this area is usually marked only by an anterior curve on the leading edge of the quadrate.

Most of the lateral surface of the quadrate forms the roughly kidney-shaped cavum tympani. This structure is covered externally by the tympanic membrane (see Baird, 1970, for references) which is attached at its edges to the quadrate and, in most cases, to the quadratojugal. "Aside from its superficial position (an external ear being absent), rather thick cutaneous layer, and more clearly circumscribed quadrate attachment, the structure of the tympanic membrane is basically similar to that in lizards" (*ibid*). The bony morphology of the cavum tympani, however, is quite different from other reptiles. In turtles the quadrate forms a wall that divides the middle ear into two regions, the cavum tympani and the cavum acustico-jugulare (see Cavum Acustico-jugulare), whereas in other reptiles the middle ear is relatively continuous. This bony wall does not appear to be developed in the Triassic *Proganochelys* (Jaekel, 1916, fig. 43). Parsons and Williams (1961, p. 91) stated: "The quadrate of

Proganochelys is, as Jaekel pointed out, very different from that of all other turtles for which this bone is known. In place of the greatly developed cavum tympani and incisura columellae auris, already so typically shown in the Jurassic turtles, we have described [*Solnhofia* and *Portlandemys*], there is only a slight incurving of the quadrate—a faint indication of things to come. Apparently there was no notch whatsoever for the columella, and the tympanum must have been attached just to the posterior edge of the quadrate instead of being for the most part bounded by that bone."

The cavum tympani is continuous posterodorsally with a variably developed space, the antrum postoticum, formed by the quadrate and squamosal (see Squamosal, for discussion of the antrum postoticum). In some turtles (e.g., *Erymnochelys madagascariensis*, and *Podocnemis unifilis*) a small concavity, termed by Williams (1954a, p. 286) the precolumellar fossa, occurs just anterior to the incisura columellae auris.

The incisura columellae auris is the opening in the quadrate traversed by the columella auris. It is quite variable in the degree to which the columella auris is enclosed by bone, particularly if fossil forms are included. As discussed above, *Proganochelys* is essentially the same as recent lizards or other reptiles in the structure of this region of the quadrate. All other known turtles, the Casichelydia, however, have some degree of closure of the incisura columellae auris. The Recent cheloniids and *Dermochelys* are examples of forms with a relatively open incisura columellae auris, while trionychids and particularly *Carettochelys*, exhibit the other extreme in which the incisura is essentially a canal surrounded by bone on all sides. Groups like the emydids show an intermediate condition in which the incisura is restricted but not completely closed posteriorly. As Siebenrock (1897, p. 288) noted, living pleurodires have both the eustachian tube and the columella auris contained in the incisura columellae auris when the incisura is closed posteriorly by bone, whereas in cryptodires the eustachian tube is excluded from the incisura when closed posteriorly. Fossil forms show ex-

ceptions, however. Baenids and meiolaniids (both considered cryptodires here) have the eustachian tube and columellae auris enclosed together by bone, whereas the Cretaceous pleurodire genera *Bothremys* and *Taphrosphys* have these structures separated by bone as in recent cryptodires.

Ventral to the cavum tympani is a block of bone, the processus articularis, that bears the articulation with the lower jaw, the condylus mandibularis. The processus articularis tends to be long in chelydrids, emydids, and testudinids; short in pleurodires and trionychids. The surface that articulates with the lower jaw is the condylus mandibularis and it is usually divided by a parasagittal furrow into two facets. In most cryptodires this furrow is matched by a longitudinal ridge on the area articularis mandibularis of the lower jaw (see Articular). Pleurodires tend to have the condylus mandibularis formed into a concave trough and the matching articulation on the lower jaw is usually hemispherical. There is some evidence (Bramble, 1971; Gaffney, 1969) that some groups of turtles (testudinids, *Podocnemis*) have the ability to protract and retract their jaws during feeding and the shape of the jaw articulation may be related to this feature.

Carettochelys is unique among turtles in having a well-developed concavity on the posterior surface of the processus articularis. Previously it was suspected that this was related to hearing (Romer, 1956) but McDowell has reported that it is the attachment site for the "posteriormost part of the pterygoideus muscle that inserts on the retroarticular process of the mandible" (1963, p. 154).

The medial surface of the quadrate (fig. 10) forms the lateral wall of the cavum acustico-jugulare and is broadly sutured to the prootic, opisthotic and pterygoid (basisphenoid in pleurodires) to obliterate most of the cranio-quadrate space (see Cavum Acustico-jugulare for discussion of this portion of the quadrate).

Just above the incisura columellae auris, in a medial view of a disarticulated quadrate, is a groove (in the lateral wall of the cavum acustico-jugulare), which bifurcates anteriorly into two grooves, a dorsal and a ventral one. The

dorsal one is the canalis stapedio-temporalis which ends anteriorly at the foramen stapedio-temporale. The area of the cavum acustico-jugulare where the canalis stapedio-temporalis originates is the aditus canalis stapedio-temporalis. The ventral groove is the lateral wall of the canalis cavernosus.

The chorda tympani branch of the facial (VII) nerve exits from the skull via a canal in the quadrate, the canalis chorda tympani quadrati. The dorsal, or internal, opening of this canal is the foramen chorda tympani superius and usually originates in the canalis cavernosus or the cavum acustico-jugulare. The ventral or external opening is the foramen chorda tympani inferius and can usually be found along the posterior surface of the processus articularis. The chorda tympani and its associated structures are absent in *Eretmochelys imbricata* and *Chelonia mydas* (Soliman, 1964, p. 255) but apparently not in other cheloniids (Poglayen-Neuwall, 1953) or other turtles. However, the canalis chorda tympani quadrati is nonetheless absent in the four genera of living cheloniids.

Pleurodires have a process of the quadrate that extends medially to meet the bony ossifications of the chondrocranium (see Cavum Acustico-jugulare). This process is readily seen in a disarticulated pleurodire quadrate and tends to have a circular concavity on its dorsal surface where it forms the floor of the cavum acustico-jugulare.

EPIPTERYGOID

Figures 11, 18, 72-80

DEVELOPMENT: The epipterygoid is a cartilage bone that ossifies in the anterior portion (processus ascendens or processus pterygoideus) of the palatoquadrate cartilage. In cryptodires portions of this cartilage usually persist in the adult (see Pterygoid, for discussion). The epipterygoid is usually lateral and somewhat dorsal to the crista pterygoidea of the pterygoid and this is the position of the cartilage in the embryo.

STRUCTURE AND CONTACTS: The epipterygoid (fig. 11) is a platelike bone that lies in the side wall of the braincase between the

parietal and the pterygoid. Pleurodires lack a distinct epipterygoid while cryptodires usually have one. The cryptodire family Baenidae (fig. 13) seems to have the epipterygoid fused to the parietal as in the adults and older individuals of many recent cryptodires. Siebenrock (1897, p. 306) reported fusion of the epipterygoid with the quadrate and pterygoid as well in some forms. *Dermochelys* is the only cryptodire definitely known to lack an epipterygoid ossification (Nick, 1912) and this would seem to be due to neoteny, as is apparently the case with other features of *Dermochelys*.

In *Trionyx* the epipterygoid comes very close to meeting the prootic above the foramen nervi trigemini and, although I do not know of any examples, I would not be surprised to find a prootic—epipterygoid contact in this area in some turtles. The posterior extension of the epipterygoid often meets the processus epipterygoideus of the quadrate.

The degree of ossification of the epipterygoid is dependent on age and may vary individually as well. The pterygoid-epipterygoid suture in particular tends to fuse with age in some individuals. Cartilaginous remnants usually persist at the anterior and posterior ends of the epipterygoid, the posterior space resulting from this in the bony skull is termed the fossa cartilaginis epipterygoidei.

The shape of the epipterygoid varies from a flat plate to a partial corkscrew. It usually is exposed on both the medial and lateral surface of the braincase but in some turtles (e.g., *Geochelone*, *sensu* Loveridge and Williams, 1957; Recent cheloniids) the processus inferior parietalis of the parietal and the crista pterygoidea of the pterygoid meet on the medial surface and the epipterygoid is a scalelike element exposed only on the lateral surface. The sutures surrounding the epipterygoid are squamous and can be quite variable and complex. In one specimen of *Chelydra serpentina* (AMNH 107387) the parietal has a narrow, thin sheet that extends ventrally to meet the pterygoid on the medial surface resulting in a suture pattern that exposes the epipterygoid in two discrete regions on this surface. The lateral surface may also be complex, particularly in the region of

the foramen nervi trigemini (see Prootic, for foramen nervi trigemini). The epipterygoid may form the anteroventral margin of the foramen (e.g., *Chelydra*) or it may be separated from the foramen by exposure of the pterygoid, the result being a complex pattern of sutures.

PTERYGOID

Figures 11-14, 16-36, 47, 53-65, 84-102

DEVELOPMENT: The complex morphology of the pterygoid can best be understood by examining the relations of this bone in the embryo. As is the case with other parts of the turtle skull, this information is based largely on Kunkel's (1912) work on *Emys orbicularis*, with supplementary information from Fuchs (1915) on *Chelonia mydas* and Shaner (1926) on *Chrysemys picta*. Again, it should be emphasized that the taxonomic breadth of developmental studies in turtles is limited to cryptodires.

The pterygoid is a membrane bone that ossifies medial and ventral to the processus pterygoideus of the palatoquadrate cartilage and roughly ventrolateral to the planum basale and trabeculae. The main features of the adult pterygoid are readily seen in the embryo. The bone is a horizontal plate with a vertical ridge, the crista pterygoidea, on the dorsal surface. Posteriorly, the horizontal part of the pterygoid lies between the quadrate portion of the palatoquadrate and the planum basale. Somewhat more anteriorly, the palatoquadrate consists of the narrow processus pterygoideus (precursor of the epipterygoid) which runs along the lateral surface of the crista pterygoidea. A rudimentary cartilago articularis is reported by Kunkel (1912, p. 752) lateral to what appears to be the processus basiptyerygoideus of the planum basale and presumably marking the position of the palatobasal articulation. Goodrich (1930, p. 423) distinguished between a palatobasal articulation as one between the palatoquadrate and trabecula (or planum basale), and a basiptyerygoid articulation as one between the parasphenoid and pterygoid bones. In turtles kinesis is lost and extensive sutural contact between the pterygoid and basisphenoid (which has part of the parasphenoid fused to it) obliterates the

articular area. Nonetheless, in the embryo rudiments of the palatobasal articulation can be seen in the form of the cartilago articularis and the processus basiptyergoideus. But even at this stage in development the pterygoid separates the palatoquadrate cartilage and the planum basale. It would be interesting to compare this stage in a cryptodire and a pleurodire, because important differences between these groups occur in this area. Unfortunately, the embryology of a pleurodire head has never been described.

The vena capitis lateralis (lateral head vein) lies on the dorsal surface of the pterygoid medial to the crista pterygoidea in a trough, the sulcus cavernosus. Another important structure, the canalis caroticus internus containing the arteria carotica interna (internal carotid artery) and the palatine branch of the facial (VII) nerve, is described by Kunkel in the chondrocranium of *Emys*. The canalis is formed beneath the processus basiptyergoideus of the planum basale (which ossifies as the basisphenoid) and dorsal to a medial extension of the pterygoid (Kunkel, 1912, fig. 20).

The pterygoid of turtles is unusual in that part of it, the dorsally projecting crista pterygoidea, is sandwiched between two cartilage bones (the epipterygoid and the basisphenoid) and forms a side wall to the braincase lateral to the primary braincase. A "new" addition to the cranial cavity of this sort is found in mammals and snakes and is termed the cavum epiptericum. This same term will be used here for turtles with the understanding that no homology to mammals or snakes is intended. The cavum epiptericum can be found in both cryptodires and pleurodires and it encloses the same area: the cranio-quadrate space and the trigeminal ganglion (see section on cavum epiptericum below).

In cryptodires most of the processus pterygoideus usually ossifies as the epipterygoid bone but in many cases part of the cartilage remains in the adult resulting in a space at either end of the epipterygoid. The posterior space is the fossa cartilaginis epipterygoidei (see Epipterygoid) but the anterior space is unnamed. The full extent of the embryonic processus pterygoideus of the palatoquadrate can

therefore be seen on the pterygoid bone in the form of the epipterygoid bone and the spaces. No information is available for the embryonic chondrocranium of pleurodires but the usual absence in the adult of both epipterygoid and palatoquadrate remnants suggests the reduction of the processus pterygoideus during development.

CONTACTS: The contacts of the pterygoid may be split into two groups: those that are present in almost all turtles and those that tend to vary among taxa. The more consistent contacts (figs. 9, 11, 76) are anteriorly with the palatine, anterolaterally with the jugal, dorsally (along the crista pterygoidea) with the processus inferior parietalis of the parietal (except in *Dermochelys*) and (in cryptodires) the epipterygoid, posteromedially with the basisphenoid, posterodorsally with the prootic, and posterolaterally with the quadrate. Cryptodires have a posterior expansion of the pterygoid, absent in pleurodires, which usually articulates with the basioccipital (but not in the Emydinae of McDowell, 1964). Pleurodires usually have an anterior contact of the processus trochlearis pterygoidei with the postorbital which does not occur in cryptodires.

The less consistent contacts of the pterygoid are concerned with a number of other bones in the skull due to the central position of the pterygoid. The presence of an anterolateral contact with the jugal is quite variable; it is typically present in most cryptodires and reduced or absent in most pleurodires. The medial contact with the other pterygoid may be lost in some forms by an expansion of the basisphenoid (Trionychidae) by a posterior enlargement of the palatines (*Carettochelys*), and by a meeting of the vomer and basisphenoid (some Baenidae). Most turtles have an anterolateral contact with the maxilla but this may be absent as in most chelonids, *Dermochelys*, and many pleurodires. All cryptodires have an epipterygoid or a persisting cartilaginous epipterygoid rudiment (*Dermochelys* and Baenoidea) on the lateral surface of the pterygoid, whereas all pleurodires lack an ossified epipterygoid and rarely have a trace of the cartilage in adults.

In many cryptodires the pterygoid extends

posteriorly and meets the exoccipital as well as the basisphenoid. In some, such as *Geochelone elephantopus*, the opisthotic also reaches the pterygoid in the region of the tuberculum basioccipitale. This contact of the pterygoid with the opisthotic and exoccipital in this area seems to be achieved by the increased ossification of cartilage in the fenestra postotica. The processus interfenestralis of the opisthotic may reach the dorsal surface of the pterygoid within the cavum acustico-jugulare as in some testudinids; but the structure is usually not ossified ventrally and the bony contact is absent in most turtles.

STRUCTURES: The basic morphology of turtle pterygoids (fig. 20) can be readily derived from captorhinomorphs or other generalized reptiles. The interpterygoid vacuity, quadrate ramus, and transverse flange (presumably homologous at least in part to the processus pterygoideus externus) of a captorhinomorph pterygoid can be recognized in *Proganochelys*. Although it is not known at present whether or not *Proganochelys* was potentially kinetic, it is clear that the Triassic form did not possess the akinetic modifications seen in the Casichelydia. The development of akinetic features was an important phase in turtle history and a study of these modifications reveals significant differences between cryptodires and pleurodires. Using the quadrate ramus as a landmark a comparison of a cryptodire and a pleurodire pterygoid shows the addition of a process posterior to the quadrate ramus in cryptodires. Removal of the pterygoid (as in figs. 18, 19) exposes much of the cranioquadrate passage and the cavum acustico-jugulare in cryptodires but not in pleurodires where this region is floored by the prootic and quadrate (see Cavum Acustico-jugulare, Quadrate, and Prootic for further discussion). This situation (and other features discussed in Gaffney, 1975d) suggests to me that cryptodires and pleurodires were already distinct lineages when these akinetic features evolved.

INTRACRANIAL STRUCTURES: The dorsal surface of the pterygoid bears a complicated series of ridges and troughs which indicate the position of a number of important structures in the

skull. The crista pterygoidea is a roughly parasagittal ridge on the dorsal surface that articulates dorsally with the processus inferior parietalis and/or the epipterygoid to form a lateral wall for the braincase and encloses a space, the cavum epiptericum. The crista pterygoidea may be used as a landmark in discussing features on the dorsal surface of the pterygoid. The area lateral to the crista lies outside the braincase in the fossa temporalis inferior, whereas the area medial to it lies in the cavum cranii.

The area inside the cavum cranii floors the remnants of the cranioquadrate space and extends between the basisphenoid and the quadrate. The vena capitis lateralis (lateral head vein) and arteria carotici interna (internal carotid artery) form prominent parasagittal sulci or canals here. The lateral head vein is housed in a trough, the sulcus cavernosus, that occurs just medial to the crista pterygoidea. The medial limits of the sulcus may be defined by a ridge on the pterygoid, as in *Chelonia*, or the sulcus may lack a pterygoid ridge, the medial limits being formed by the basisphenoid and/or prootic, as in *Chelus*. The posterior part of the sulcus cavernosus is enclosed dorsally by the prootic and called the canalis cavernosus. The anterior opening of the canalis cavernosus is termed the foramen cavernosum and is usually formed by the pterygoid and prootic. Just anterior to this structure the trigeminal nerve ganglion overlies the sulcus cavernosus and transmits branches V_2 and V_3 of the trigeminal nerve from the foramen nervi trigemini to the fossa temporalis inferior. In most cryptodires the mandibular artery also exits via the foramen nervi trigemini, whereas in pleurodires it does not. The foramen nervi trigemini is usually formed by the crista pterygoidea of the pterygoid ventrally and the prootic and parietal dorsally. In some cases the epipterygoid and quadrate may form a portion of the structure with the pterygoid contribution reduced (e.g., *Trionyx*) or absent (e.g., *Kinosternon*) (see Prootic for detailed discussion).

THE CANALIS CAROTICUS INTERNUS AND ASSOCIATED STRUCTURES: The arteria carotici interna (internal carotid artery) is contained

within the canalis caroticus internus which is formed principally by the pterygoid and basisphenoid. The foramen anterior canalis carotici interni is the anterior opening of the canalis caroticus internus and the position where the internal carotid artery enters the cavum cranii. In all turtles this opening is formed by the basisphenoid (see Basisphenoid for discussion). The foramen posterior canalis carotici interni is the posterior opening of the canalis and is usually formed by the pterygoid in cryptodires. The foramen is often formed ventrally by the pterygoid but completed dorsally by the cartilage occupying the fenestra postotica. In some forms, such as cheloniids and trionychids, the pterygoid may form all of the foramen posterior canalis carotici interni.

In all cryptodires, except the baenoids, the foramen posterior canalis carotici interni is in the vicinity of the posterior edge of the pterygoid and the canalis caroticus internus trends medially to enter the basisphenoid. In baenoids the foramen posterior canalis carotici interni occurs on the medial edge of the pterygoid about midway along the basisphenoid-ptyergoid suture, and the canalis caroticus internus is, therefore, shorter in these forms. Pleurodires lack the posterior expansion of the pterygoid found in cryptodires and the foramen posterior canalis carotici interni is not found in the pterygoid (except in *Podocnemis* where the foramen is essentially obliterated due to the development of a chamber for a portion of the M. pterygoideus; see below).

The canalis caroticus internus may be contained within the pterygoid, as in living cheloniids, it may be partially contained within the pterygoid, as in *Trionyx*, or it may be formed between the pterygoid-basisphenoid suture, as in *Geochelone*. In most turtles the canalis caroticus internus has a series of associated canals that are formed mostly by the pterygoid and contain the arteria palatinus, the palatine (vidian) branch of the facial (VII) nerve and smaller branches of these structures. The morphology of these canals and their contents is of considerable interest because they form the basis of some current ideas about cryptodire relationships. There are two main

canals that branch off the anterolateral wall of the canalis caroticus internus; the more lateral one is the canalis nervi vidiani and the more medial one the canalis caroticus lateralis. These will be discussed below.

THE CANALIS CAROTICUS LATERALIS AND ASSOCIATED STRUCTURES: The canalis caroticus lateralis is a branch of the canalis caroticus internus that extends anteriorly in the pterygoid or, more often, in the basisphenoid-ptyergoid suture to open in the floor of the sulcus cavernosus just lateral to the rostrum basisphenoidale. This anterior opening is the foramen caroticum laterale. This canal and foramen usually transmit the arteria palatina (palatine artery) a branch of the internal carotid artery that runs forward into the orbital—nasal area. In most cryptodires the canalis caroticus lateralis, foramen caroticum laterale and the palatine artery are minute but usually visible. The small palatine artery has been reported for the following forms: *Graptemys geographica*, *Chrysemys scripta*, *Chrysemys picta*, *Gopherus berlandieri*, *Testudo graeca*, *Ocadia sinensis*, *Chinemys reevesi*, *Clemmys insculpta*, and *Chelydra serpentina* (McDowell, 1961); *Chrysemys scripta*, *Terrapene carolina* (Albrecht, 1967); *Gopherus polyphemus*, *Chelydra serpentina*, and *Macrocllemys temminckii* (Albrecht, 1976). A relatively small or absent canalis caroticus lateralis and foramen caroticum laterale is the condition in all the remaining cryptodires with the important exceptions of the Trionychidae, Kinosternidae (*sensu* Wermuth and Mertens, 1961), Dermatemydidae and living Cheloniidae.

The trionychids, kinosternids, and dermatemydids are all characterized by having a relatively large foramen caroticum laterale and canalis caroticus lateralis. Dissection of *Kinosternon subrubrum* and *Sternotherus odoratus* (McDowell, 1961); *Trionyx spinifer*, *Trionyx muticus*, *Lissemys punctata*, *Kinosternon subrubrum*, *Sternotherus odoratus*, and *Sternotherus minor* (Albrecht, 1967) have shown the arterial differences associated with the change in canal and foramen size. In the kinosternids the palatine artery is large and supplies the nose and orbit as well as a branch to

the mandible, whereas in trionychids the foramen caroticum laterale contains only a large mandibular artery with the rest of the palatine artery absent. The pseudopalatine artery appears to be a functional replacement for the palatine artery (Albrecht, 1967). The morphology of the canalis caroticus lateralis also differs in these groups from the "typical" cryptodires. The canalis itself is much shorter, nearly nonexistent in trionychids, and the foramen caroticum laterale is lateral to the sella turcica and dorsum sellae rather than being more anterior as in emydids (see Gaffney, 1975d, for further discussion).

One of the most characteristic specializations of the cheloniid skull is the absence of a bony roof for the anterior portion of the canalis caroticus internus and for the entire canalis caroticus lateralis. In most turtles the branching of the palatine artery from the internal carotid artery takes place surrounded by bone but in cheloniids and *Dermochelys* (Nick, 1912; Albrecht, 1976) the internal carotid artery leaves the canalis caroticus internus and enters the cranial cavity before giving off the palatine artery. It would therefore appear that in cheloniids the anterior portion of the roof of the canalis caroticus internus and the entire roof of the canalis caroticus lateralis is missing. The internal carotid artery enters the sella turcica by going through a foramen, apparently the foramen anterius canalis carotici interni, that is simply a hole in the basisphenoid (see Basisphenoid). As the canalis caroticus lateralis is not present as a canal, strictly speaking its point of exit into the cranial cavity, the foramen caroticum laterale is also absent. However, Albrecht (1976) has argued that the opening of the canalis caroticus internus into the sulcus cavernosus should probably be called the foramen caroticum laterale because it would appear that it has migrated posteriorly. Albrecht (*ibid*) has also favored the use of the term sulcus caroticus for the floor of the area traversed by the internal carotid artery after it leaves the canalis caroticus internus and enters the cranial cavity. Again, this area is not strictly homologous with the sulcus cavernosus but rather with the floor of the anterior portion

of the canalis caroticus internus of other turtles. I would extend the use of the term sulcus caroticus to include the anterior continuation of the groove where it is traversed by the palatine artery, anterior to its separation from the more medial internal carotid artery. This groove is usually termed the sulcus cavernosus but, if the above interpretation is correct, the groove is actually the floor of the canalis caroticus internus (in part) and the canalis caroticus lateralis. The sulcus caroticus, then, would occur in living cheloniids and *Dermochelys*, although the situation in the latter genus is obscured by the more prominent absence of ossification in many cranial structures.

In living chelonoids the palatine artery is equal or larger in diameter than the internal carotid artery (Nick, 1912; McDowell, 1961; Albrecht, 1967, 1976) but this condition is distinctly different from trionychoids in which the stapedia artery is reduced and the bony canalis caroticus lateralis is retained.

In pleurodires, Albrecht (1976) has reported that the canalis caroticus lateralis and foramen caroticum laterale are absent in *Pelomedusa* and *Pelusios*, but they are present in *Podocnemis* (including *Erymnochelys* and *Peltocephalus*) and most chelids (except *Chelus*). However, among the forms he dissected, the palatine artery was absent in all but *Podocnemis sextuberculata*, in which a vestigial palatine artery was found. The vidian nerve traversed the canalis caroticus lateralis in most of the chelids he dissected (*Batrachemys nasuta*, *Chelodina longicollis*, and *Platemys platycephala*) but the function of the canalis caroticus lateralis in the other *Podocnemis* specimens was not apparent. The foramen caroticum laterale of *Podocnemis* is relatively large apparently due to its position at the anterior end of the hypertrophied pterygoideus muscle chamber.

The canalis carotico-pharyngealis is a small canal directed ventrally from the canalis caroticus lateralis and containing the arteria carotico-pharyngealis. The canal is formed by the pterygoid and emerges on the ventral surface of that bone as the foramen carotico-pharyngeale. It is reported in *Chrysemys* and *Sternotherus*

but it is absent in *Trionyx* (Albrecht, 1967).

THE CANALIS NERVI VIDIANI AND ASSOCIATED STRUCTURES: The path of the facial (VII) nerve and its branches is complex and known in only a relatively few turtles. The following treatment is based primarily on Soliman (1964) and Albrecht (1967, 1976) and the terminology follows Soliman. The path of the facial nerve through the prootic is described under Prootic. In cryptodires the facial nerve forms the geniculate ganglion (ganglion geniculi) as it enters the canalis cavernosus. At this point two nerves emerge from the ganglion, the ramus posterior (or hyomandibular) which extends posteriorly in the canalis cavernosus (in cryptodires) and the ramus palatinus (or vidian) which goes anteriorly. In cryptodires the ramus posterior travels posteriorly in the canalis cavernosus until it reaches the columella auris where it splits into the dorsal ramus hyoideus and the ventral chorda tympani (see Quadrate and Cavum Acustico-jugulare for further description of these areas, and Soliman, 1964, for more detailed information on the nerve components). In pleurodires the geniculate ganglion is apparently not contained in the canalis cavernosus and the ramus posterior is contained in the prootic (see Prootic).

The foramen pro ramo nervi vidiani is an opening or short canal connecting the canalis caroticus internus with the canalis cavernosus. The anterior branch (called both vidian and palatine) of the facial nerve travels through this foramen as it leaves the geniculate ganglion in the canalis cavernosus and travels to the canalis caroticus internus. The foramen pro ramo nervi vidiani occurs only in cryptodires (see Prootic) and is usually formed by both prootic and pterygoid, although in some forms (e.g., *Macrolemys*) it is formed entirely by the pterygoid.

Siebenrock (1897) and most later authors have described the palatine (vidian) nerve as leaving the canalis caroticus internus via its own canal and extending anteriorly until it exits from the canal in the vicinity of the foramen palatinum posterius. More recent work by Soliman (1964) and Albrecht (1967, 1976), however, indicates a greater degree of com-

plexity and variation in the course of this nerve. Because of the differences in scope of these papers, complete understanding of this complexity is still lacking. Albrecht's study is aimed at the bony structures and arterial contents and he describes them in detail but does not identify the nerve branches involved, while Soliman describes the nerves in detail but does not precisely indicate their relationship to bony structures (this is also due to the immature nature of his specimens which are still cartilaginous in some critical areas). *Pseudemys scripta* (*Chrysemys scripta* of McDowell, 1964) appears to be the most generalized of the three forms studied by Albrecht and the following account is from his description of this species (Albrecht, 1967, p. 87) . . . "From this foramen, [foramen pro ramo nervi vidiani] some nerves enter a small, anterolaterally directed canal in the pterygoid which goes lateral and parallel to the canalis caroticus internus anteriorly to the region of the canalis carotico-pharyngealis; for convenience, I call this nerve canal the posterior canalis nervi vidiani. Other nerves exit from the foramen pro ramo nervi vidiani and traverse the canalis caroticus internus anteriorly to enter the canalis caroticus lateralis. These nerves then divide; some branches go through the canalis caroticus lateralis and exit on the dorsal surface of the pterygoid bone whereas other nerves go ventrally, entering the canalis carotico-pharyngealis with the posterior canalis nervi vidiani. These nerves in the bony canals then enter the anterior canalis nervi vidiani which goes through the pterygoid and palatine bones from the region of the canalis carotico-pharyngealis to the foramen palatinum posterius; the nerves then traverse this foramen to enter the orbit." The nerves described by Albrecht are all portions of the vidian (palatine) nerve. Soliman (1964, p. 250) described the nerves in this area in *Chelydra*. In addition to nerves, most of the vidian canals contain small arteries described by Albrecht.

EXTRACRANIAL SURFACES OF THE PTERYGOID: All the structures discussed above are found medial to the side wall of the braincase (formed primarily by the processus inferior parietalis and the crista pterygoidea) or within

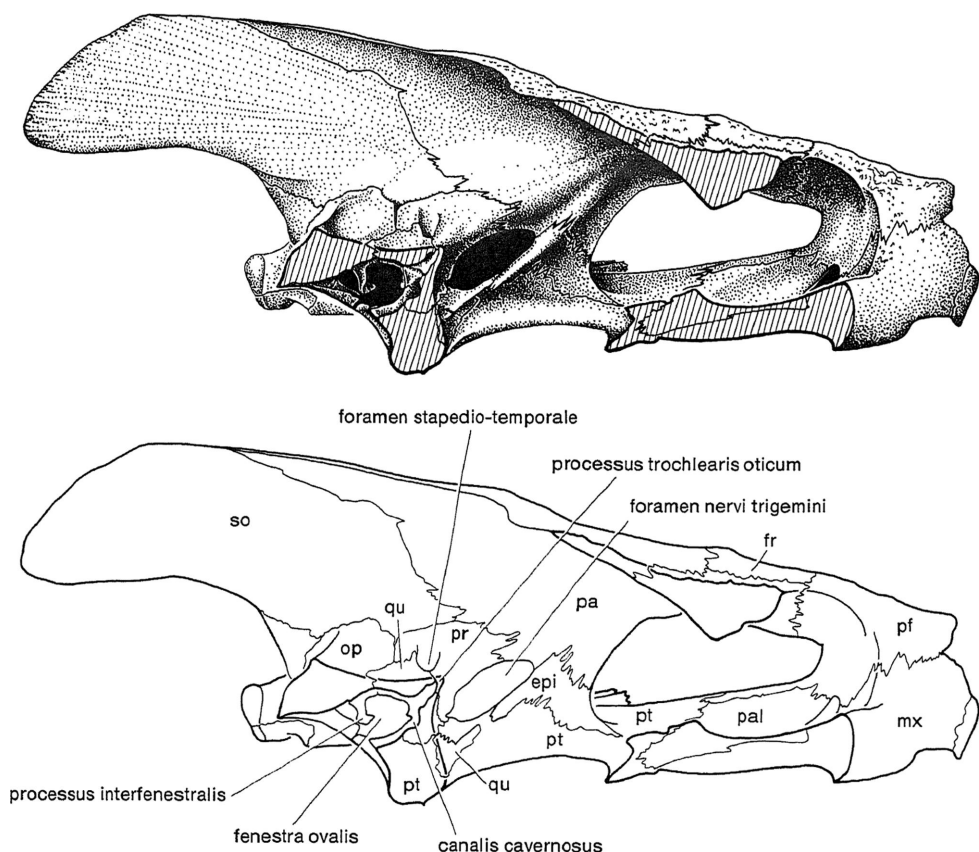


FIG. 11. *Chelydra serpentina* (AMNH 9249), Chelydridae, East Hampton, Suffolk County, New York. Lateral view of skull with a parasagittal section on right side removed to show ethmoid region and processus trochlearis oticum. Hatching indicates cut surfaces, compare with figure 12. From Gaffney (1975d).

the pterygoid bone itself. The dorsal surface of the pterygoid lateral to the crista pterygoidea and the ventral surface bear structures that are mostly involved with the jaw mechanism and are described below.

The processus pterygoideus externus is a lateral process of the pterygoid found only in cryptodires, that extends around the anteromedial edge of the fossa temporalis inferior and has a lateral edge usually produced into a vertical plate. The processus appears to be comparable, if not homologous, with the transverse pterygoid flange found in captorhinomorphs and other reptiles. The vertical plate on the lateral edge of the processus is similar to one found in lizards and other Recent reptiles. This plate is usually covered with cartilage and oral mucosa and apparently acts as a

guide for the lower jaw (see mundplatte discussion below). In cryptodires the processus may be reduced, as in *Geochelone*, or the vertical plate may be enlarged and extended posteriorly as in *Trionyx*.

The processus trochlearis pterygoidei is a lateral extension of the pterygoid into the fossa temporalis inferior, which supports the cartilago transiliens of the bodenaponeurosis (main adductor tendon or external tendon of Schumacher, 1973, and earlier references). The processus is found only in pleurodires. The main adductor tendon of turtles runs over a trochlea that changes the line of action of the tendon from a generally fore-aft one to a more dorsoventral one. The position of the trochlea is marked on the tendon by a meniscus-shaped cartilage, the cartilago transiliens. The position

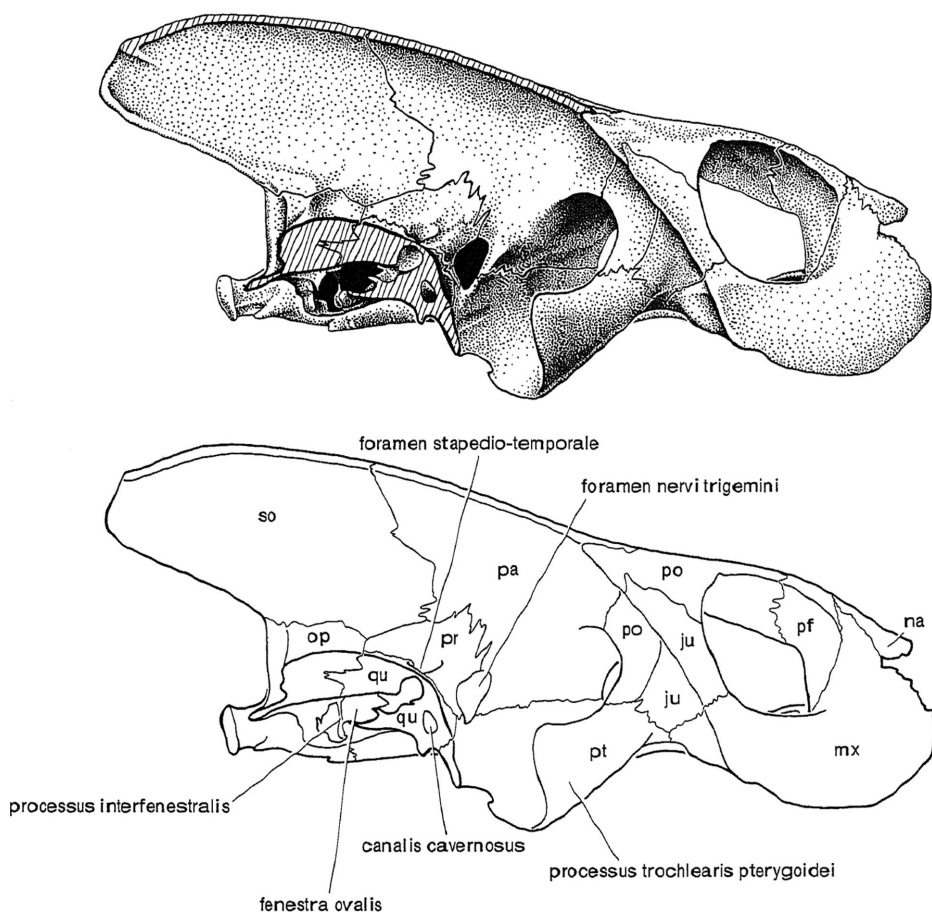


FIG. 12. *Emydura* sp. (AMNH 72418), Chelidae, no data. Lateral view of skull with a parasagittal section on right side removed to show ethmoid region and processus trochlearis pterygoidei. The latter structure projects lateral to the plane of the section. Hatching indicates cut surfaces, compare with figure 11. From Gaffney (1975d).

of the trochlea is an important difference between cryptodires and pleurodires. In cryptodires the trochlea is on the otic chamber (the structure is termed the processus trochlearis oticum, see Prootic), whereas in pleurodires the trochlea is on the pterygoid (see Processus trochlearis pterygoidei). The function of the trochlea appears to be the same but its structure is not homologous in the two groups.

The size and orientation of the processus trochlearis pterygoidei varies somewhat. In *Podocnemis* the processus is large and directed laterally while in *Chelus* and *Chelodina* it is reduced and directed posteriorly. Other

pleurodires fall between these two, with pelomedusids tending to have the processus better developed than chelids. Bramble (MS) has suggested that this is related to the relative stress borne by the pterygoid during feeding. There is a correlation between the degree of lateral projection of the processus and the extent to which the basisphenoid and quadrate join to buttress the pterygoid. Forms such as *Podocnemis*, which are presumed to have higher stress on the pterygoid during feeding, have a processus that projects laterally and a broad contact between the quadrate and the basisphenoid-basioccipital. In chelids, such as *Chelus* and

Chelodina, the pterygoid stress is presumed to be relatively less (due to the more carnivorous habits of the latter; *Podocnemis* is believed to be more herbivorous) and the processus projects posteriorly and the quadrate-basisphenoid articulation is lost or reduced. (I am indebted to Dr. Dennis Bramble for bringing this to my attention via a manuscript he is presently working on).

The soft tissues around the processus trochlearis pterygoidei are also interesting in a comparison of pleurodires and cryptodires. Fuchs (1932) studied this region in embryos of *Podocnemis expansa*, *Emys orbicularis* (*E. europaea* of Fuchs), and *Eretmochelys imbricata* (*Chelone imbricata* of Fuchs). He found a fold of oral mucosa in the angle of the mouth that contained glandular cells and he named this the ductus angularis oris. In *Podocnemis* the ductus is greatly enlarged into a blind pocket that extends over the anterolateral surface of the processus trochlearis pterygoideus between the bone and cartilago transiliens. Fuchs noted the presence of a rudimentary ductus angularis oris just lateral to the vertical plate of the processus pterygoideus in two cryptodires.

Examination of this area in turtles and other reptiles suggests to me that the ductus angularis oris is the same as the mundplatte ("mouth plate") of other authors. In *Iguana* "the ventral border of the skin of the infratemporal area turns under this ligament [the quadratomaxillary ligament], is covered by mucous membrane, and forms a recess, the mundplatte, which is the angle of the mouth, and continues anteriorly as the coronoid recess. The medial layer of the mundplatte continues ventrally as the skin of the lower jaw. Dorsally, the mundplatte receives the insertion of the levator angularis oris muscle" (Oelrich, 1956, p. 40). In *Varanus* Frazetta (1962, pp. 296, 304) described the structure and function of the mundplatte. During mouth opening the mundplatte pocket is everted, whereas during adduction the levator angularis oris "insures that the excess skin will be folded neatly beneath the [quadratomaxillary] ligament and within the cavity of the mundplatte" (*ibid.*, p. 304). Thus the glandular mucosa of the

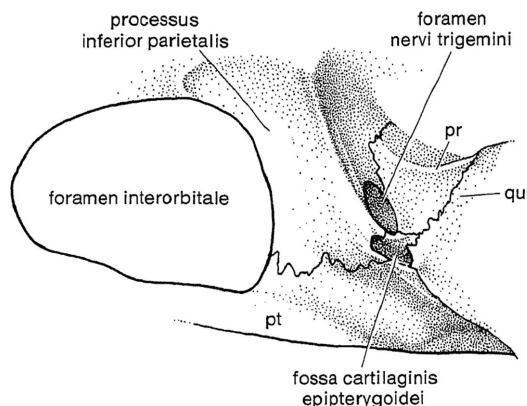


FIG. 13. *Chisternon undatum* (AMNH 5961), Baenidae, Bridger Formation, Eocene, Grizzly Buttes West, Wyoming. Left ethmoid region, anterior on lefthand side of page. Epipterygoid is absent as a distinct ossification but a well-developed fossa cartilaginosa epipterygoidei is present.

mundplatte apparently acts as a guide for the coronoid process of the lower jaw during adduction. In cryptodires this function can also be surmised and the mundplatte in this group is directly comparable to that structure in other reptiles. In pleurodires, however, what appears to be the mundplatte (=ductus angularis oris) is extended dorsally and posteriorly, presumably to act as a lubricating agent for the cartilago transiliens.

The equation of the mundplatte and ductus angularis oris of pleurodires suggests homologizing the processus pterygoideus externus of cryptodires with the processus trochlearis pterygoidei of pleurodires. Both structures lie medial to the mundplatte and lateral to the M. pterygoideus and occur on comparable areas of the pterygoid. (For further discussion of the morphology and possible phylogenetic significance of the pterygoid and jaw muscle morphology in cryptodires and pleurodires see Gaffney, 1975d).

CAVUM EPIPTERICUM: "The cavum epiptericum . . . is an extracranial space situated laterally to the side wall of the orbitotemporal region of the skull, dorsally to the basitrabecu-

lar process, and medially to the processus ascendens of the pterygoquadrate cartilage" (DeBeer, 1937, p. 430). The space is found in a number of vertebrates and is typically traversed by the vena capitis lateralis (lateral head vein) and the profundus (V) branch of the trigeminal nerve. In most vertebrates the cavum epiptericum has a medial wall that separates it from the cavum cranii proper but in turtles the cavum epiptericum is included in the bony skull by the absence of a medial wall and the development of a bony lateral wall. This lateral wall consists dorsally of the processus inferior parietalis and ventrally of the crista pterygoidea with the addition of the epipterygoid in most cryptodires.

In turtles the cavum contains the lateral head vein and a number of nerves running anteriorly

to the orbital region. The optic (II), oculomotor (III), trochlearis (IV), and abducent (VI) nerves all traverse the cavum epiptericum. The abducent (VI) nerve innervates the rectus eye muscles that attach more or less within the cavum epiptericum. The other soft structures lying in the ventral region of the cavum are discussed under the pterygoid bone as they usually are surrounded at least in part by that element.

In cheloniids the lateral wall is reduced and replaced by cartilage, whereas in *Dermochelys* the bony processus inferior parietalis is rudimentary and the cavum epiptericum lacks a lateral bony wall. In addition, due to the absence of the dorsal roof of the canalis caroticus lateralis in cheloniids, the palatine artery traverses the cavum epiptericum in this group (see Pterygoid, canalis caroticus lateralis).

BRAIN CASE ELEMENTS

SUPRAOCCIPITAL

Figures 4, 11, 12, 37, 38, 41-43, 52, 66-102

DEVELOPMENT: The supraoccipital is a cartilage bone that ossifies in the tectum synoticum (tectum posterius of Kunkel). Most reptiles have epiotic ossification centers in the otic capsules that fuse with the supraoccipital. Contrary to Shaner (1926, p. 358), there is no evidence that epiotics exist in turtles; nonetheless, the supraoccipital ossification includes the dorsal one-third of each otic capsule.

The anterior portion of the tectum tends to remain cartilaginous in the adult and forms a small portion of the inner surface of the cavum cranii. Zangerl (1960, p. 290) and Gaffney and Zangerl (1968, p. 228) drew attention to the ridge formed in the endocranial casts due to the loss of this cartilage in the dried or fossilized skull.

CONTACTS: The supraoccipital has extensive contact with the posteromedial margins of the parietals. This contact usually is overlapping in nature with the parietal extending posteriorly over the supraoccipital. Anteroventrally, there is a contact on either side with each prootic;

whereas posteroventrally there is a contact with each opisthotic. The prootic-opisthotic-supraoccipital suture is usually more or less Y-shaped and somewhat cartilaginous, at least internally where it forms part of the wall of the cavum labyrinthicum. The posteroventral limits of the supraoccipital, near the foramen magnum, usually contact the exoccipitals.

Siebenrock (1897) has noted the laterally expanded ventral portion of the supraoccipital in *Terrapene*. In this form the occurrence of a well-developed squamosal and supraoccipital results in the meeting of these bones in a long suture in the floor of the fossa temporalis superior that excludes the contacts usually seen in this area. Internally, beneath the squamosal the supraoccipital contacts the quadrate also.

In meiolaniids (*Crossochelys*, Simpson, 1938) and an undescribed Miocene podocnemine (Bramble, MS) the squamosal contacts the supraoccipital. In both cases the supraoccipital is somewhat expanded but much more so in *Crossochelys* (see Temporal Emargination) where the supraoccipital, parietal and squamosal form the margins of a true temporal fenestra.

STRUCTURES: The supraoccipital (fig. 104) is an unpaired median element lying in the post-erodorsal region of the skull. It forms the dorsal margin of the foramen magnum, the dorsal portion of the cavum labyrinthicum and most of

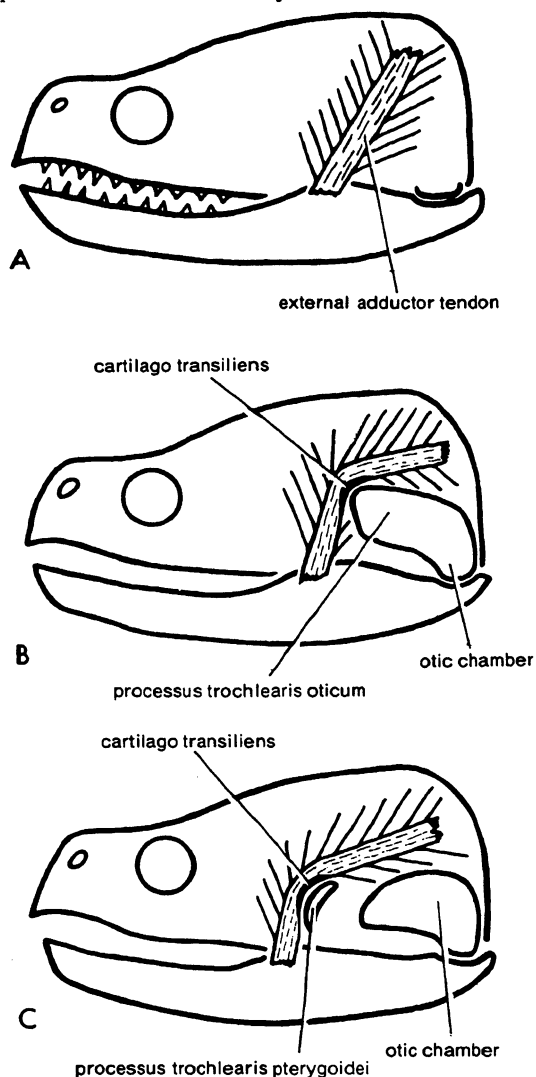


FIG. 14. A comparison of the external adductor tendon in non-chelonian reptiles (A), cryptodiran turtles (B), and pleurodiran turtles (C). The size and shape of structures are indicated diagrammatically. From Gaffney (1975d).

the crista supraoccipitalis. It is shaped like an inverted Y in cross section with three plates of bone meeting along the midline.

The most prominent external feature of the supraoccipital is the crista supraoccipitalis. This is a vertically oriented plate sometimes extending posteriorly beyond the occipital region. It serves as the attachment site for the *M. adductor mandibulae externus pars profundus* of Schumacher (1954, 1955a, 1955b, 1973). Schumacher (*ibid.*) has shown that in trionychids and *Podocnemis expansa* the posterior tip of the crista supraoccipitalis serves as the attachment site for a series of tendon lobes (supraoccipitales Sehnenblatt) that are interleaved between laminae of the main adductor tendon (see especially Schumacher, 1955b, plate VI, figs. 1, 2). This tendon is apparently associated with an increase in length of the crista supraoccipitalis.

The variation in size of the crista supraoccipitalis is considerable in turtles. Trionychids, *Podocnemis*, some testudinids, and some emydids have a very well-developed crista supraoccipitalis, whereas chelids, *Dermochelys*, *Plesiochelys*, and baenids are forms with a relatively small crista supraoccipitalis. In *Chelus* the crista is actually formed in part by the expanded dorsal section of the exoccipitals. Nonetheless, compared with other reptiles turtles may be characterized as having a prominent crista supraoccipitalis.

The vertical sheet of bone forming the crista supraoccipitalis is joined along its ventral edge by a horizontal sheet of bone in some forms. Although a rudimentary development of this structure may be seen in some testudinoids, such as *Geochelone* (*sensu* Loveridge and Williams, 1957) it is best seen in *Podocnemis* and trionychids with its greatest development being in *Carettochelys*. In this genus the horizontal sheet of the crista supraoccipitalis extends the full length of the crista and is wider than the vertical sheet is deep. In a juvenile specimen of this genus (AMNH 85893) the lateral edges of the horizontal sheet of the crista supraoccipitalis are split horizontally

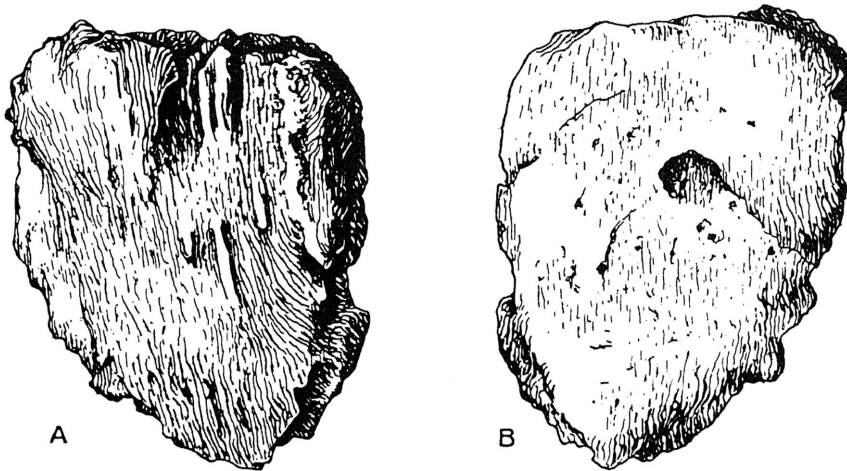


FIG. 15. Os transiliens of *Gopherus polyphemus* (MCZ 45695, approximately X10), Testudinidae. A. Dorsal view. B. Ventral view. This bone is the ossified cartilago transiliens that occurs in the main adductor tendon or Bodenaponeurosis of turtles (from Ray, 1959).

which suggests that it may represent partial ossification of the supraoccipital tendon described by Schumacher (*ibid.*)

The supraoccipital has paired ventrolaterally projecting processes that form the roof of the cavum labyrinthicum (see Cavum Labyrinthicum). The recessus labyrinthicus supraoccipitalis contains the membranous common crus. The indentations or canals formed by the dorsal portions of the anterior and posterior semicircular ducts (Baird, 1960, 1970) are the canalis semicircularis anterior and canalis semicircularis posterior respectively. A notch or foramen in the medial wall of the supraoccipital portion of the cavum labyrinthicum is the foramen aquaducti vestibuli, which carries the endolymphatic duct from the otic sac in the cavum cranii to the sacculus in the cavum labyrinthicum (Baird, 1960, 1970). The hiatus acusticus is usually limited dorsally by the supraoccipital (again, see Cavum Labyrinthicum).

The supraoccipital is usually exposed in the dorsal part of the foramen magnum. This exposure, however, is reduced in some forms such as *Podocnemis expansa* and may be lost entirely as in *Chelodina* and *Chelus* (see Exoccipital). The supraoccipital also forms a varying

amount of the posterior roof of the cavum cranii.

EXOCCIPITAL

Figures 37-43, 47-50, 53-102

DEVELOPMENT: The exoccipital is a cartilage bone that ossifies in the arcus occipitalis of the chondrocranium. The exoccipital forms the posterior margin of the foramen jugulare anterius which is the adult equivalent of the fissura metotica. Ventrally the ossification extends into the dorsolateral portion of the condylus occipitalis where it meets the basioccipital. The exoccipital ossification also includes most of the foramina nervi hypoglossi which lie at the posterolateral edge of the planum basale in the embryonic chondrocranium.

CONTACTS: The exoccipital (figs. 41-43) is a paired bone lying lateral to the foramen magnum and forming part of the condylus occipitalis. It is sutured dorsally to the supraoccipital, anterodorsolaterally to the opisthotic, and ventromedially to the basioccipital. This is also the condition in *Captorhinus* (Permian) and most other reptiles. Many cryptodires, however, also have a ventrolateral contact with the pterygoid, seen in trionychids and chelonids and slightly developed in many testudinoids.

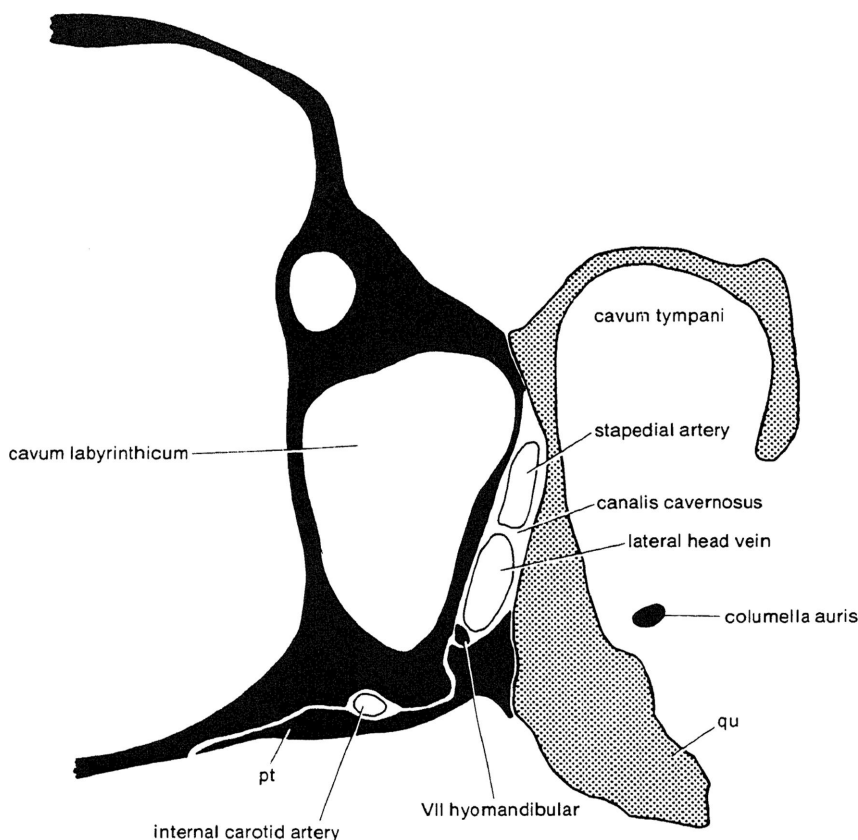


FIG 16. *Chelydra serpentina* (UT Chely 68), Chelydridae, no data. Transverse section through ear region of a cryptodire. Quadrate stippled. Skull midline on left. See figure 17. From Gaffney (1975d).

STRUCTURES: Parsons and Williams (1961, p. 66) described the exoccipital as being "in two main parts, a dorsolateral and a ventromedial. The dorsal portion is a rather narrow bar of bone lying posterior and ventromedial to the opisthotic. Dorsomedially, it possesses a short suture with the supraoccipital and forms the dorsolateral margin of the foramen magnum, and ventrolaterally it lies along the dorsomedial margin of the fenestra postotica. From near the center of this dorsal bar, a strong process extends ventromedially to the basioccipital. Medially, this process forms the ventrolateral margin of the foramen magnum, and laterally it enters into the medial margin of the fenestra postotica." Although intended for Jurassic cryptodires, this description holds true for most turtles.

The formation of the condylus occipitalis is variable in turtles but the exoccipitals usually participate (see Basioccipital). The exoccipitals may meet in the midline at the base of the foramen magnum and prevent dorsal exposure of the basioccipital on the condylus occipitalis, as in *Chelydra*, or the basioccipital may be exposed dorsally for the length of the condylus, as in *Podocnemis expansa*, *Dermochelys*, and some cheloniids. In some forms (e.g., *Pelusios*, *Pelomedusa*, *Taphrosphys*, and *Carettochelys*) the basioccipital lacks a contribution to the condylus and this structure is made up entirely of the exoccipital, while in *Corsochelys* (Zangerl, 1960, p. 288) the exoccipitals do not form any of the condylus occipitalis.

The vagus (X) and accessory (XI) nerves and the vena cerebialis posterior pass through

the skull in the region lateral to the exoccipital (see Cavum Acustico-jugulare). This bone forms foramina in varying degrees for the passage of these structures. The foramen jugulare anterius is the opening that carries the above structures from the cavum cranii into the recessus scalae tympani portion of the cavum acustico-jugulare. This foramen is usually formed by the opisthotic anteriorly and the exoccipital posteriorly. Its anteroventral edge may be finished in cartilage (*Podocnemis expansa*) thereby preventing an opisthotic-exoccipital contact at this point. Lateral to the foramen jugulare anterius is the recessus scalae tympani. The contribution of the exoccipital to the formation of this chamber is variable. The exoccipital usually forms at least the posteromedial margin of the recessus scalae tympani and in

Chelydra it forms most of the floor of the recessus. The vena cerebialis posterior and vagus (X) nerve can be followed through the region of the recessus scalae tympani to their point of exit from the skull (the foramen jugulare posterius and the fenestra postotica respectively). Although the morphological position of the exit of these structures does not seem to vary, the degree to which this exit is ossified does vary among turtles (see Cavum Acustico-jugulare).

The hypoglossal nerve (XII) is a complex of fibers that leave the brain stem just anterior to the foramen magnum via two or three short canals termed the foramina nervi hypoglossi. Although the exoccipital usually forms most or all of the foramina, the basioccipital may form the ventral margin and if a third foramen is

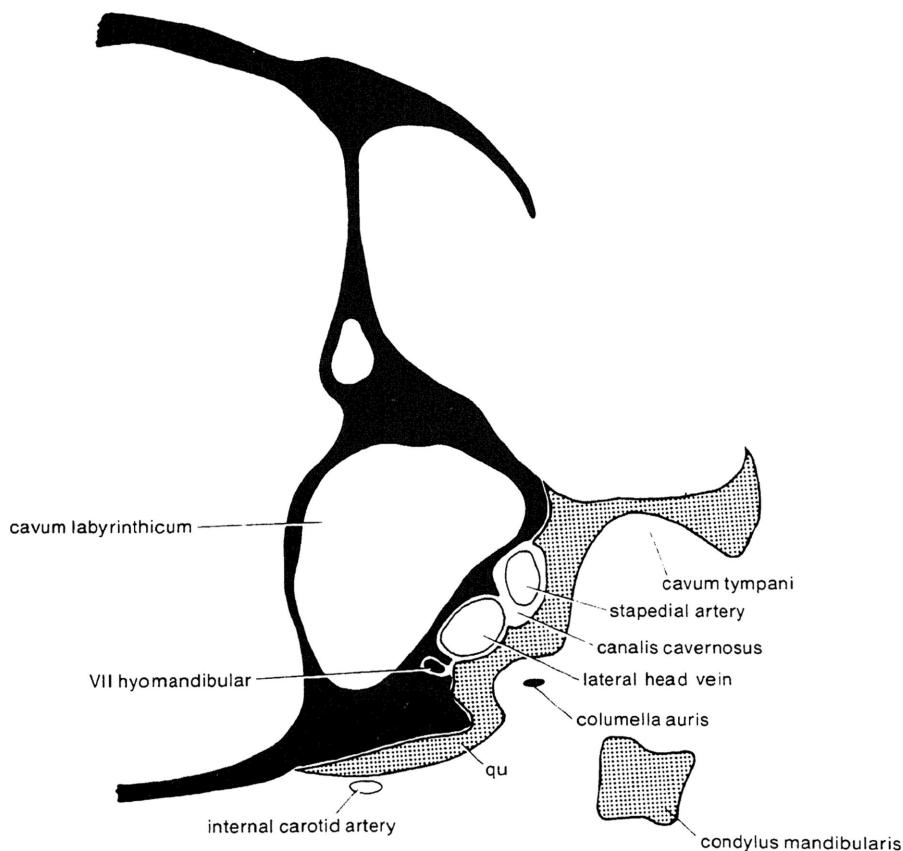


FIG. 17. *Podocnemis expansa* (UT POD III 211), Pelomedusidae, no data. Transverse section through ear region of a pleurodire. Quadrate stippled. Skull midline on left. See figure 16. From Gaffney (1975d).

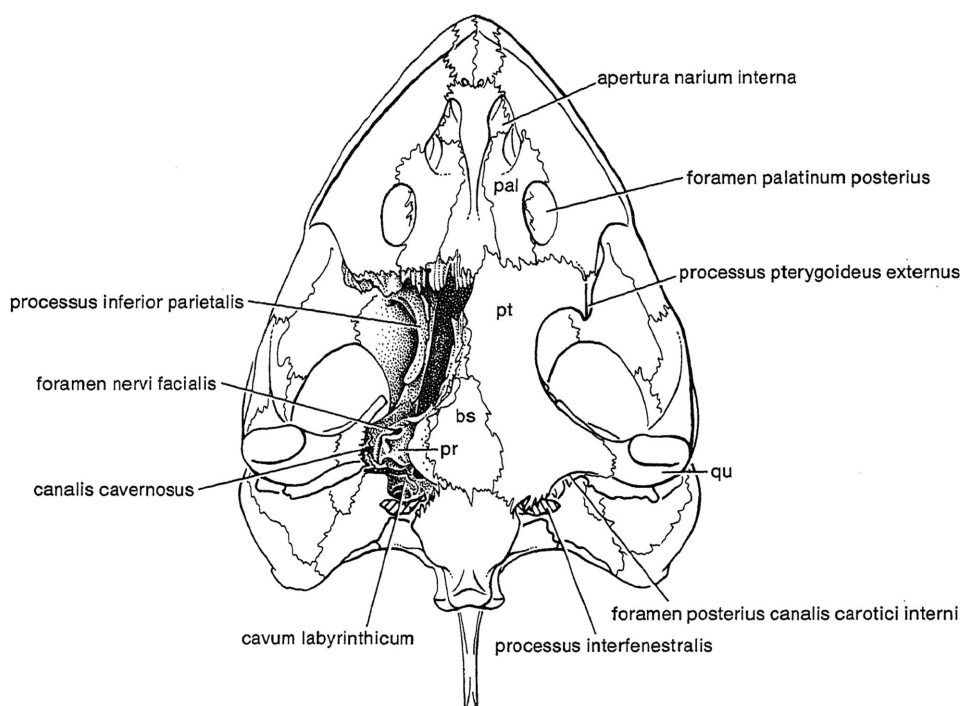


FIG. 18. *Chelydra serpentina* (AMNH 110446), Chelydridae, no data. Ventral view of a cryptodire with the right pterygoid removed; stippling shows sutural areas and structures covered by pterygoid. Processus interfenestralis of opisthotic indicated by diagonal lines for a landmark. See figure 19. From Gaffney (1975d).

present it is often formed mostly by the basioccipital (fide Siebenrock, 1897). Sometimes (e.g., *Caretta*) when three foramina are present medially, the anterior two combine and only two exit on the outside of the skull. Bojanus (1819), Shiino (1913), Ogushi (1913), and Soliman (1964) described the branches of the hypoglossal nerve and its components. The foramina emerge from the skull just lateral to the condylus occipitalis and medial to the foramen jugulare posterius.

BASIOCCIPITAL

Figures 39-44, 47, 48, 53-102

DEVELOPMENT: The basioccipital is a cartilage bone that ossifies from paired centers in the posterior half of the planum basale. Presumably, the fenestra basicranialis posterior, the large median opening in the planum basale, roughly separates basisphenoid from basioccipi-

tal portions. Shaner (1926, p. 358) reported that two thin lamellae of membrane bone become incorporated into the anterior part of the ventral surface of the basioccipital.

CONTACTS: The contacts of this bone, particularly in the area of the condylus occipitalis are difficult to determine in adults, as the sutures fuse with age (Siebenrock, 1897, p. 250). In all turtles the anterior edge of the basioccipital meets the basisphenoid and the lateral margins are sutured to the exoccipitals. In most turtles the opisthotic reaches the anterodorsolateral edge of the basioccipital, although the suture is often filled with a thick cartilage pad. In most cryptodires (with the exception of the Emydinae of McDowell, 1964) the pterygoids reach the anterolateral edge of the basioccipital on the ventral side. This contact may be quite extensive as in trionychids or more limited as in *Malaclemys*.

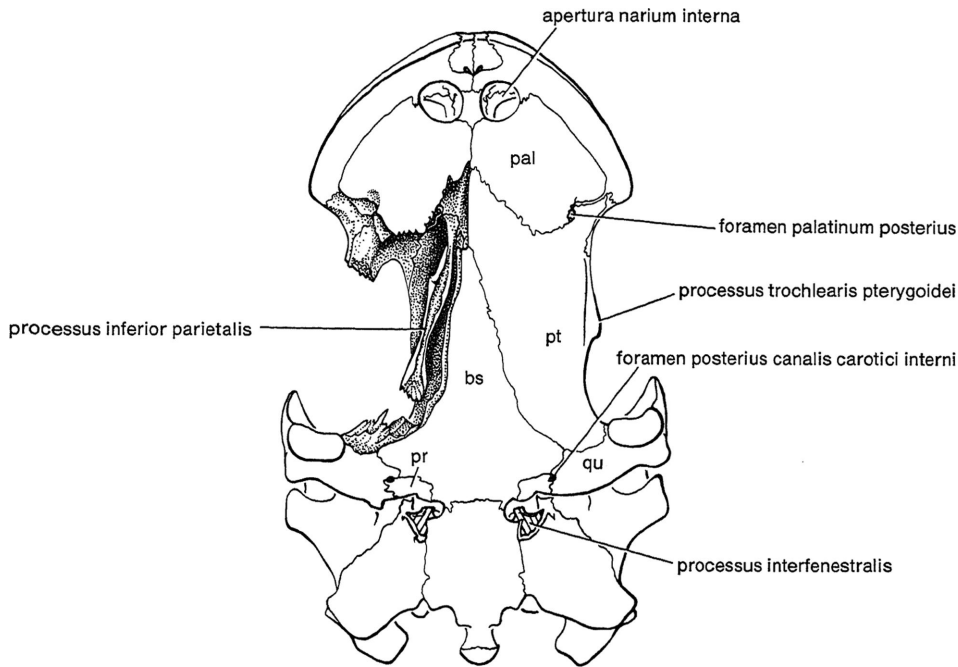


FIG. 19. *Chelodina* sp. (AMNH 108954), Chelidae, Darwin area, Northern Territory, Australia. Ventral view of a pleurodire with the right pterygoid removed; stippling shows sutural areas and structures covered by pterygoid. Processus interfenestralis of opisthotic indicated by diagonal lines for a landmark. See figure 18. From Gaffney (1975d).

STRUCTURES: The basioccipital is a roughly triangular element lying at the posteroventral edge of the skull, on the midline and just below the foramen magnum. The dorsal surface of the basioccipital forms a sagittal trough and is part of the floor of the cavum cranii. A median ridge, the crista dorsalis basioccipitalis is variably developed in most turtles, but is absent in some forms (*Podocnemis expansa* and *Trionyx ferox*, for example). At the anterior edge of this ridge an oval tubercle, the basis tuberculi basalis may be formed on the suture between the basisphenoid and basioccipital. Kesteven (1910, p. 376) indicated that the "bifid ligament of the medulla" attaches to this tubercle. The dorsolateral margin of the basioccipital may form part of the ventral edge of the foramina nervi hypoglossi (as in *Trionyx* and *Malaclemys*) but these structures are formed mostly by the exoccipital.

The extent to which the ventral end of the processus interfenestralis contacts the basioccipital is variable in turtles but in most turtles there is a well-developed contact. The Emydinae of McDowell (1964), however, are characterized by a reduction of this contact caused by a loss of the lateral margin of the basioccipital. McDowell hypothesized that the loss of this lateral tuberosity (the batagurine process) is a derived character uniting the Emydinae and that in the Batagurinae the reduction had not taken place. The batagurine process can be identified by the following characteristics listed in their order of importance as I interpret this from McDowell: extends lateral to lagena (this can only be roughly determined from the bony skull), forms floor of recessus scalae tympani, and is in contact with paracapsular sac (this is also difficult to determine from the dried skull).

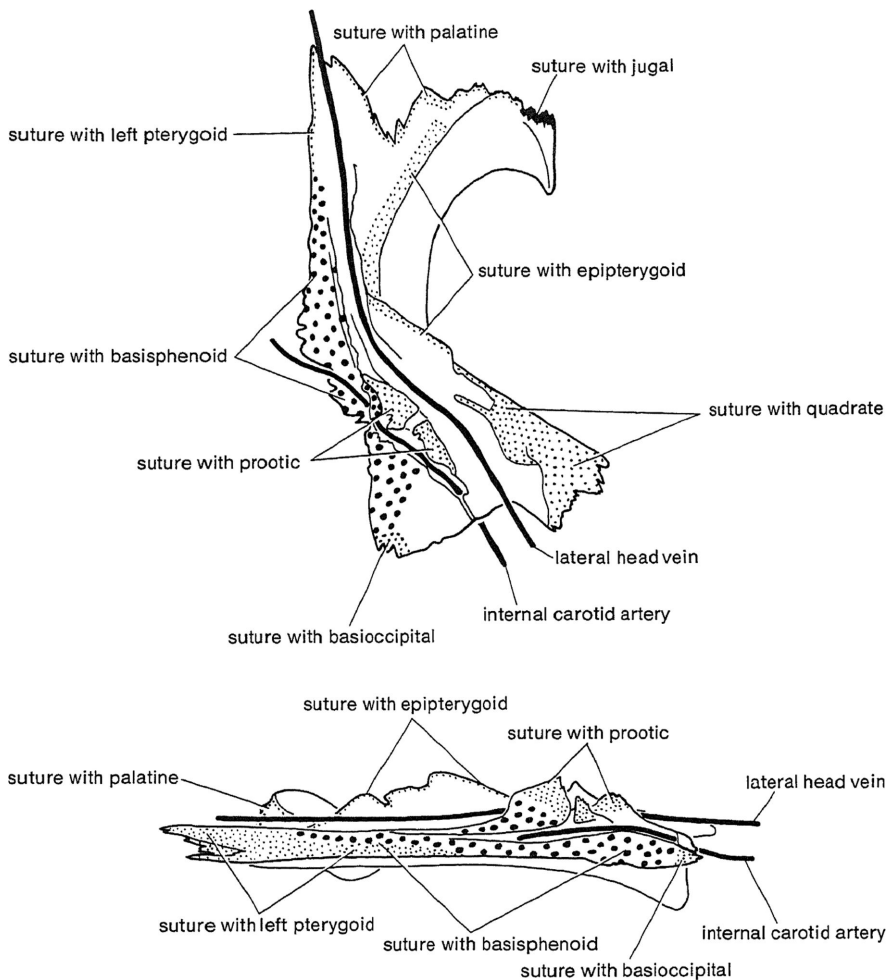


FIG. 20. Diagrammatic views of a right pterygoid of *Chelydra serpentina* showing the major bone contacts and structures. Upper, dorsal view; lower, medial view (anterior on left). This figure is intended as an aid to interpreting the following figures of pterygoids (figs. 21-29).

The ventral aspect of the basioccipital may lack surface features (e.g., *Pelusios*) or it may have a series of rugosities and depressions for muscular attachments (e.g., *Emydura*). The most prominent rugosities for muscle attachment are the paired tubercula basioccipitalia. These structures may be reduced as in *Malaclemys* or greatly developed as in *Carettochelys*. The tuberculae are usually made up of approximately equal contributions of the basioccipital and exoccipitals. The ventral surface of the basioccipital may have a trough

(*Trionyx*) or semicircular depression (*Podocnemis expansa*) opening ventrally and/or posteriorly for the attachment of muscles. This may be absent as in *Pelusios*.

The basioccipital usually makes up the ventral third of the condylus occipitalis. In *Pelusios*, *Pelomedusa*, *Taphrosphys* (Late Cretaceous) and *Carettochelys*, however, the basioccipital lacks a contribution to the condylus occipitalis (see Exoccipital), while in *Corsochelys* (Zangerl, 1960, p. 288) the basioccipital forms all of the condylus.

PROOTIC

Figures 11-14, 18, 19, 34, 37-40, 50-83

DEVELOPMENT: The prootic is a cartilaginous bone that ossifies in the anterior half of the otic capsule. Anteriorly, the ossification includes the commissura praefacialis and the path of the facial nerve as it leaves the brain (VII). The medial surface of the otic capsule usually remains unossified so that at least one of the acoustic (VIII) nerve foramina is not formed in bone. The interior of the capsule is also more or less cartilaginous (see Cavum labyrinthicum).

CONTACTS: Anterodorsomedially, the prootic has a parasagittal contact with the processus inferior parietalis, except in *Dermochelys* where the parietal lacks a descending process. Posterodorsomedially, there is a suture with the supraoccipital and posteriorly with the opisthotic (on the dorsal surface of some forms, e.g., baenids, the supraoccipital may prevent opisthotic and prootic contact). In *Chelus* the exoccipital contacts the prootic posteroventrally. The lateral surface of the prootic abuts against the quadrate and ventromedially the prootic is sutured to the basisphenoid. In all turtles except *Dermochelys* the pterygoid contacts the anteroventrolateral portion of the prootic and in cryptodires it covers the ventral surface of the prootic as well. Pleurodires lack the "cryptodire flange" of the pterygoid (see Pterygoid and Cavum acustico-jugulare) and usually have the prootic exposed ventrally. The podocnemine group and *Bothremys* (Late Cretaceous) have other specializations in this area which result in a ventrally covered prootic.

STRUCTURES: The prootic (figs. 105, 109) usually contributes to the formation of the processus trochlearis oticum of cryptodires. This structure usually forms an anteriorly directed prominence on the otic chamber and bears a synovial joint for articulation with the cartilago transiliens of the main adductor tendon system of cryptodires (Schumacher, 1954, 1955a, 1955b, 1956, 1973). The degree of development of the processus is quite variable, reaching an extreme in such forms as the trionychids and being most reduced in the cheloniids and *Dermochelys*. The position of the processus

trochlearis oticum reflects the point where the main adductor tendon changes from movement in a primarily horizontal direction to movement in a more vertical plane. The cartilago transiliens is present as an ossification (os transiliens, fig. 15) in Recent and fossil gopher tortoises (Ray, 1959; Legler, 1962; Bramble, 1974, discussed functional aspects).

Pleurodires lack a processus trochlearis oticum but instead have a functionally equivalent trochlea on the pterygoid, the processus trochlearis pterygoidei (see Pterygoid). Pelomedusids seem to approach the condition seen in some Recent cheloniids in which the prootic lacks a well-developed processus trochlearis oticum and the difference between the two groups seems to be one of degree. Nonetheless, this is not the case as dissection demonstrates that the cartilago transiliens is present in cheloniids on the prootic but in pelomedusids it is on the pterygoid. A further osteologic feature of this area in cryptodires is the presence of surface rugosities and concentrated nutrient foramina where the cartilago transiliens attaches to the otic chamber. This roughened condition is not seen in pleurodires (further discussion of the morphology of this area and its phylogenetic implications may be found in Gaffney, 1975d).

The prootic and quadrate usually share in the formation of the processus trochlearis oticum but in some cases the quadrate may form most of the processus (as in *Chelydra*) or the prootic may be the dominant element (e.g., *Pelochelys* and *Solnhofia*, Gaffney, 1975c). In some trionychids the parietal forms the medial portion of the processus and in *Testudo graeca* (Loveridge and Williams, 1957, fig. 21) the prootic is completely excluded from the processus trochlearis oticum by contact of the quadrate and parietal.

On the dorsal surface of the otic chamber lies the foramen stapedio-temporale which is the outer opening of the canalis stapedio-temporalis and contains the stapedia artery (see also Quadrate and Cavum acustico-jugulare). The canalis is always formed by the quadrate and prootic, but due to the overlapping of various bony sheets on top of the otic chamber the make up of the foramen stapedio-temporale is

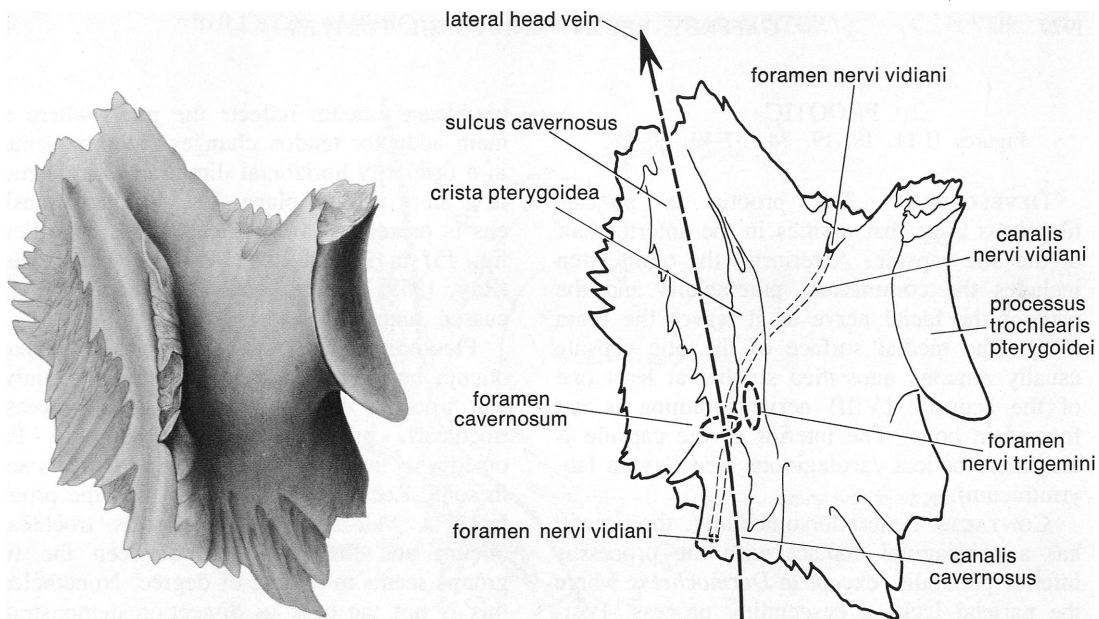


FIG. 21. *Pelomedusa subrufa* (AMNH 63581), Pelomedusidae, south of Soalala, Malagasy Republic. Dorsal view of right pterygoid. Pterygoid length 9 mm.

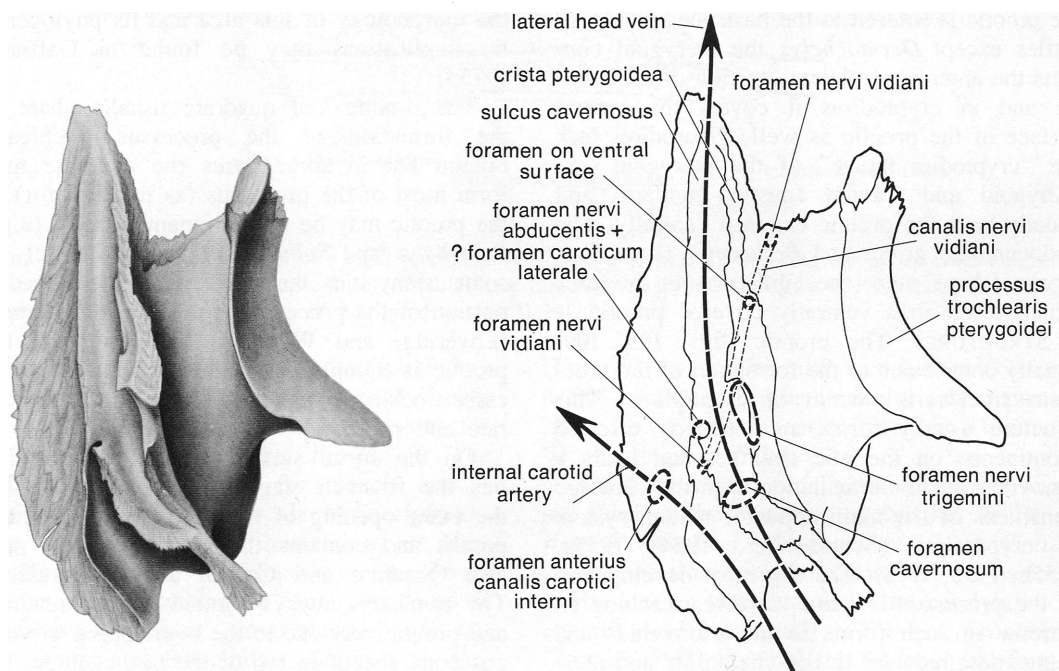


FIG. 22. *Podocnemis unifilis* (AMNH 58200), Pelomedusidae, no data. Dorsal view of right pterygoid. Pterygoid length 33 mm.

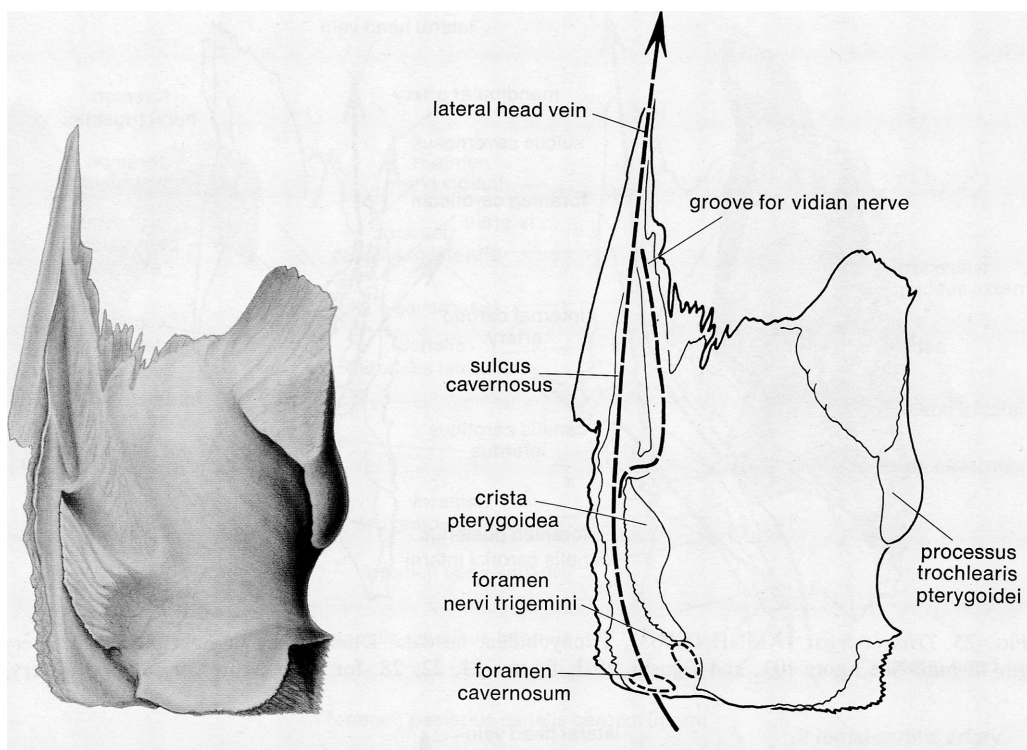


FIG. 23. *Chelus fimbriata* (AMNH 111962), Chelidae, no data. Dorsal view of right pterygoid. Pterygoid length 54 mm. Compare with *Chelodina* in Siebenrock, 1897, figure 32.

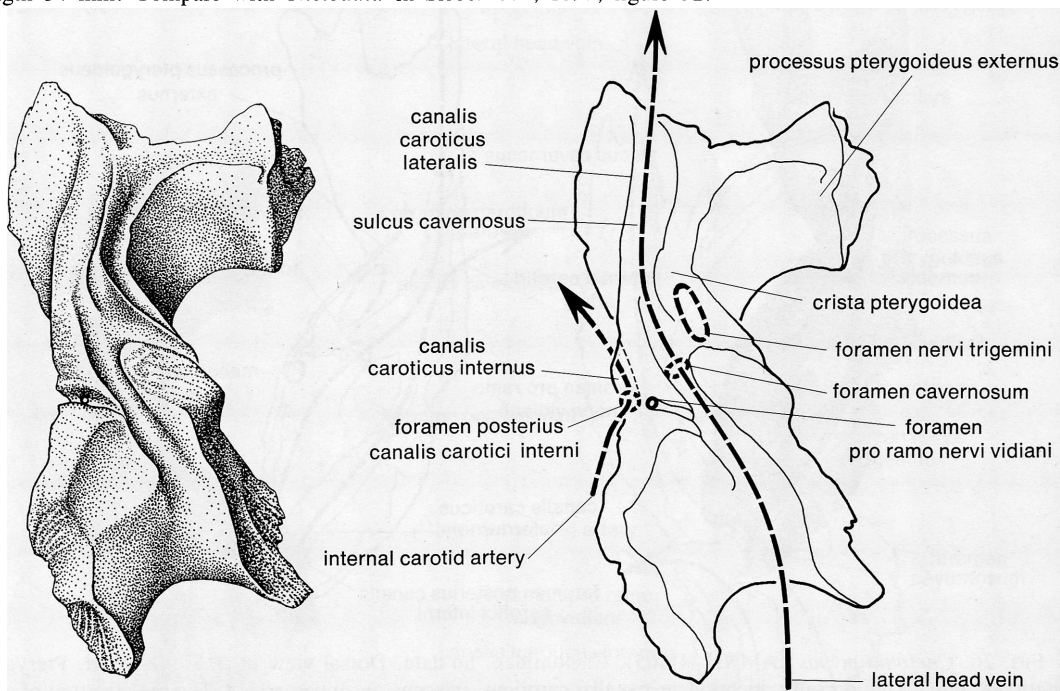


FIG. 24. Family Baenidae, genus indeterminant, Hell Creek Formation, Late Cretaceous, Bug Creek Anthills, McCone County, Montana. Dorsal view of right pterygoid. Pterygoid length 25 mm. Based on MCZ 3563 with added information from MCZ 3566. From Gaffney (1975d).

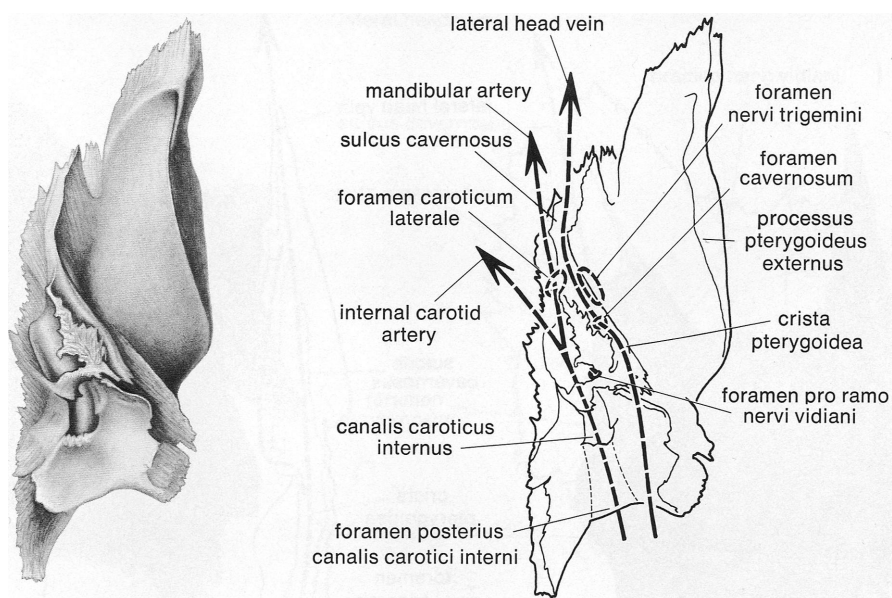


FIG. 25. *Trionyx ferox* (AMNH 111963), Trionychidae, no data. Dorsal view of right pterygoid. Pterygoid length 48 mm. See figure 103, and Ogushi, 1911, figures 21, 22; 28, for other figures of a *Trionyx* pterygoid.

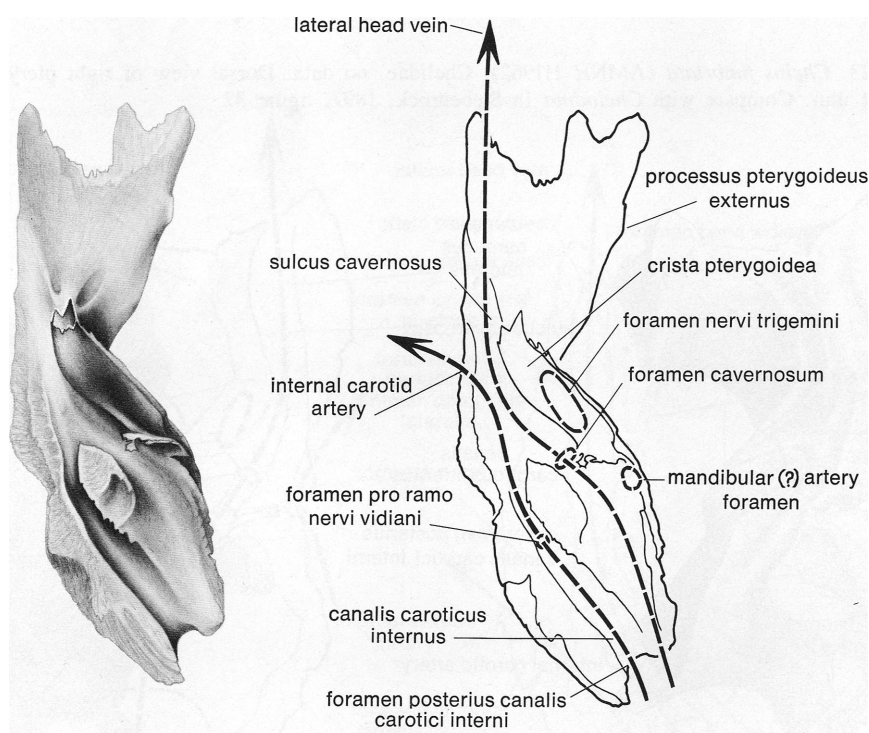


FIG. 26. *Chelonia mydas* (AMNH 111965), Cheloniidae, no data. Dorsal view of right pterygoid. Pterygoid length 48 mm. The dorsally incomplete canalis caroticus internus is apparently a juvenile feature of this specimen because in larger skulls the canalis is completely formed by the pterygoid. The position of the foramen pro ramo nervi vidiani is indicated from adult specimens and it lies above the internal carotid artery which does not traverse the foramen. See Siebenrock, 1897, figure 37; and Kesteven, 1910, figures 36, 37, for figures of adult *Chelonia* pterygoids.

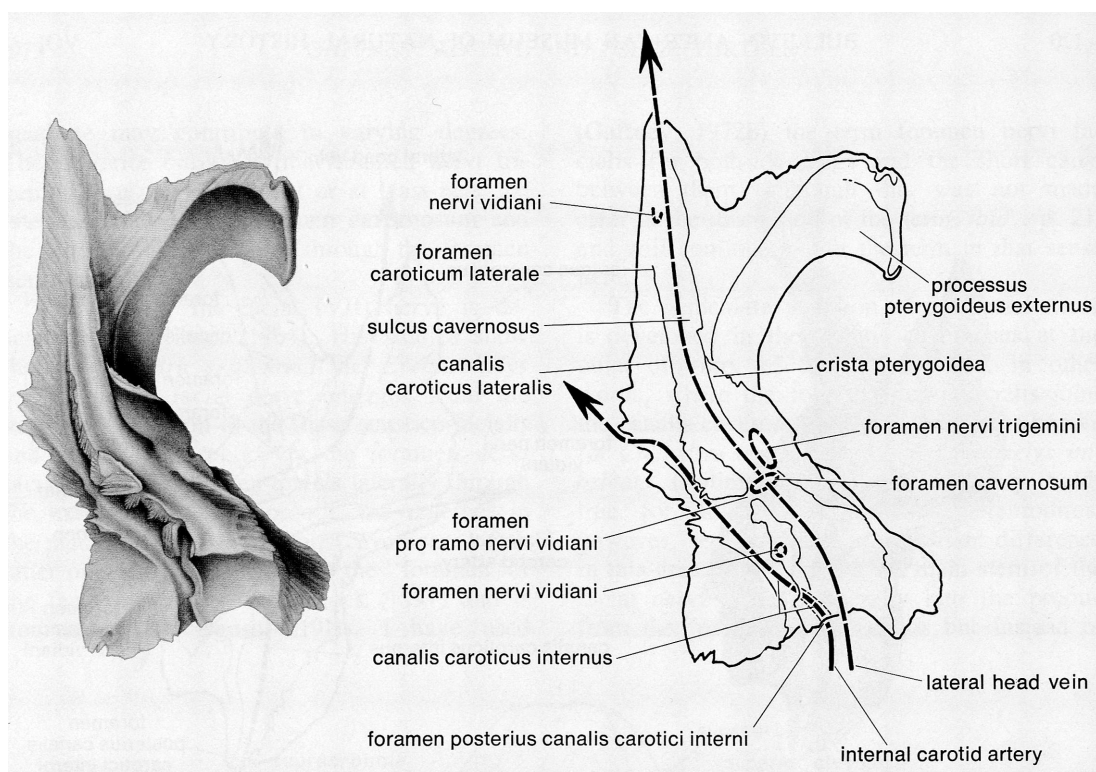


FIG. 27. *Chelydra serpentina* (AMNH 107388), Chelydridae, no data. Dorsal view of right pterygoid. Pterygoid length 35 mm. See Siebenrock, 1897, figure 33, for another figure of a *Chelydra* pterygoid.

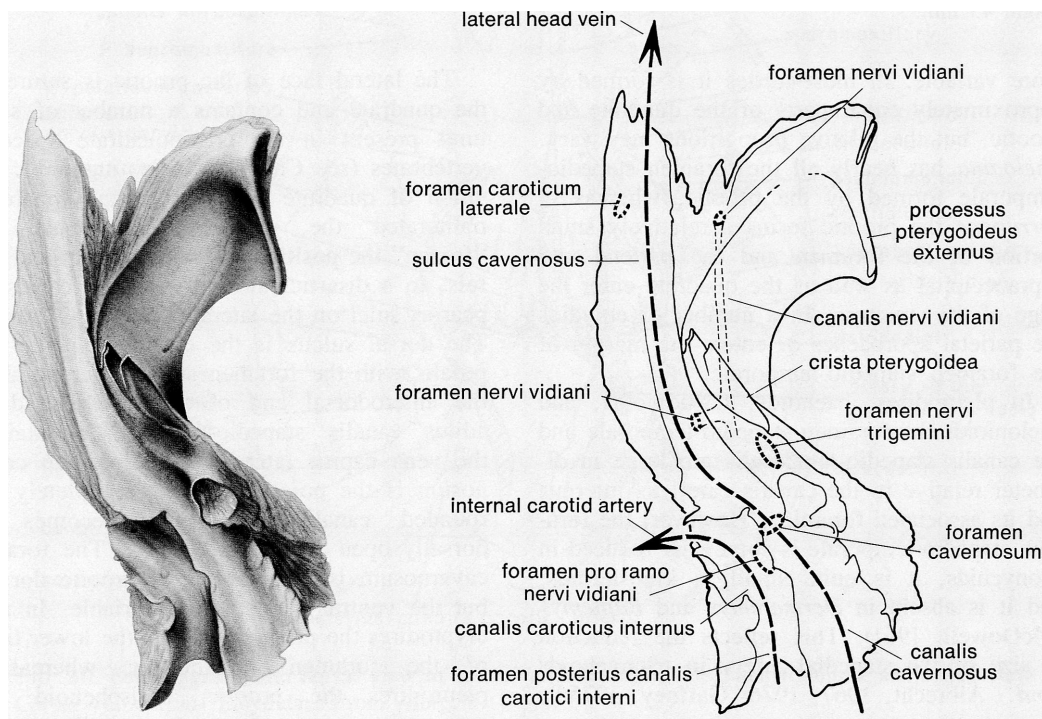


FIG. 28. *Chrysemys scripta* (AMNH 111961), Emydidae, no data. Dorsal view of right pterygoid. Pterygoid length 8 mm. For other emydid pterygoids see Siebenrock, 1897, figures 34, 36, 38.

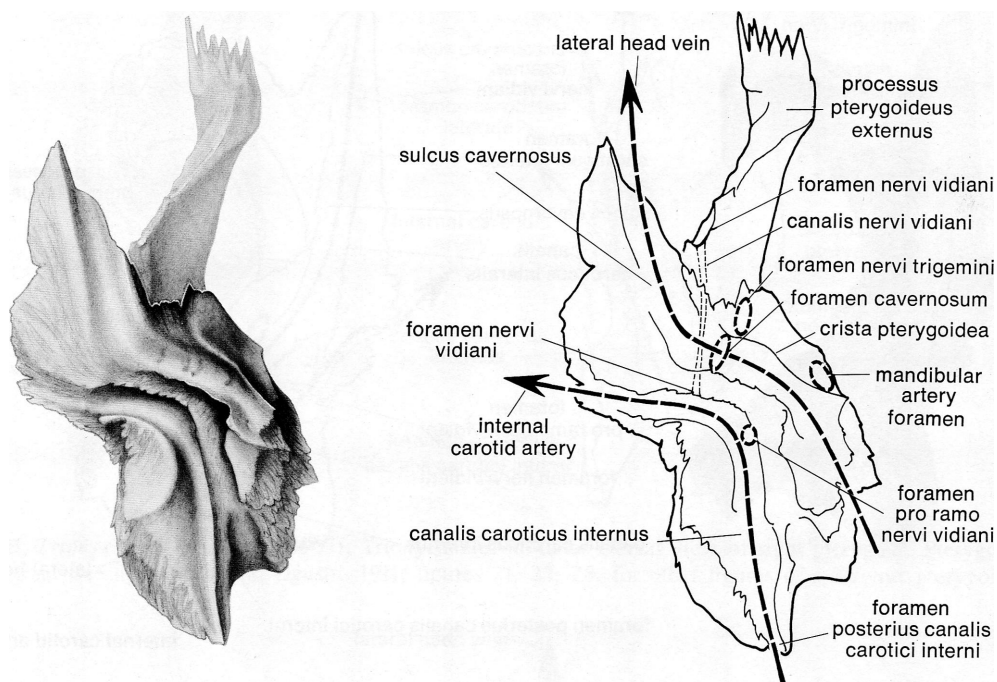


FIG. 29. *Geochelone* sp. (AMNH 111966), Testudinidae, no data. Dorsal view of right pterygoid. Pterygoid length 43 mm.

more variable. In most turtles it is formed by approximately equal parts of the quadrate and prootic, but the relative proportions may vary. *Chelodina* has nearly all the foramen stapedio-temporale formed by the prootic, whereas in *Terrapene* the prootic forms a relatively small portion of the foramen and the parietal and supraoccipital as well as the quadrate enter the edge of the structure. In a number of emydids the parietal approaches or enters the margin of the foramen stapedio-temporale.

In pleurodires, baenoids, testudinoids, and chelonoids the foramen stapedio-temporale and the canalis stapedio-temporalis are large in diameter relative to the canalis caroticus internus and its associated foramina. However, the foramen stapedio-temporale is somewhat reduced in trionychids, it is quite small in kinosternids, and it is absent in *Dermatemys* and *Baptemys* (McDowell, 1961). This reflects the reduction in size of the stapedia artery in trionychoids (*ibid.*, Albrecht, 1967, 1976; Gaffney, 1975d).

The lateral face of the prootic is sutured to the quadrate and contains a number of structures present in the cranioquadrate space of vertebrates (see Cavum acustico-jugulare). The union of quadrate and prootic has apparently obliterated the cranioquadrate space and "frozen" the position of certain nerves and vessels. In a disarticulated prootic two canals appear as sulci on the lateral face (see Quadrate). The dorsal sulcus is the canalis stapedio-temporalis with the foramen stapedio-temporale at the anterodorsal end of the canalis and the aditus canalis stapedio-temporalis containing the vena capitis lateralis. The foramen cavernosum is the point where the completely surrounded canalis cavernosus becomes the dorsally open sulcus cavernosus. The foramen cavernosum is formed by the prootic dorsally but the ventral elements are variable. In most cryptodires the pterygoid forms the lower limits of the foramen cavernosum, whereas in pleurodires the prootic, basisphenoid, and

quadrate may contribute in varying degrees. The posterior border of the foramen nervi trigemini is usually confluent or at least near the lateral border of the foramen cavernosum and the latter is usually visible through the foramen nervi trigemini.

The path of the facial (VII) nerve is described by Soliman (1964). His studies show that in *Chelydra serpentina* and *Eretmochelys imbricata* the facial nerve emerges from the vestibular ganglion in the fossa acustico-facialis and enters the prootic via the foramen nervi facialis. The nerve then travels laterally through the main body of the prootic and emerges in the medial wall of the canalis cavernosus. This latter opening is called simply the "foramen for the facial nerve" by Siebenrock (1897) and is not named by Ogushi (1911). I have used

(Gaffney, 1972b) the term foramen nervi facialis for both openings and the short canal between them (although this was not made clear in the discussion of the term, *ibid.*, p. 21) and will continue to use the term in that sense here.

The geniculate ganglion of the facial nerve is developed in the canalis cavernosus at the point of entry of the facial nerve, in other words, where the foramen nervi facialis joins the canalis cavernosus. This condition is known for *Chelydra serpentina* and *Eretmochelys imbricata* (Soliman, 1964) and probably holds true for all other cryptodires. Pleurodires, however, seem to have an important difference in this area. In this group the main stem of the facial nerve extends laterally into the prootic from the fossa acustico-facialis but instead of

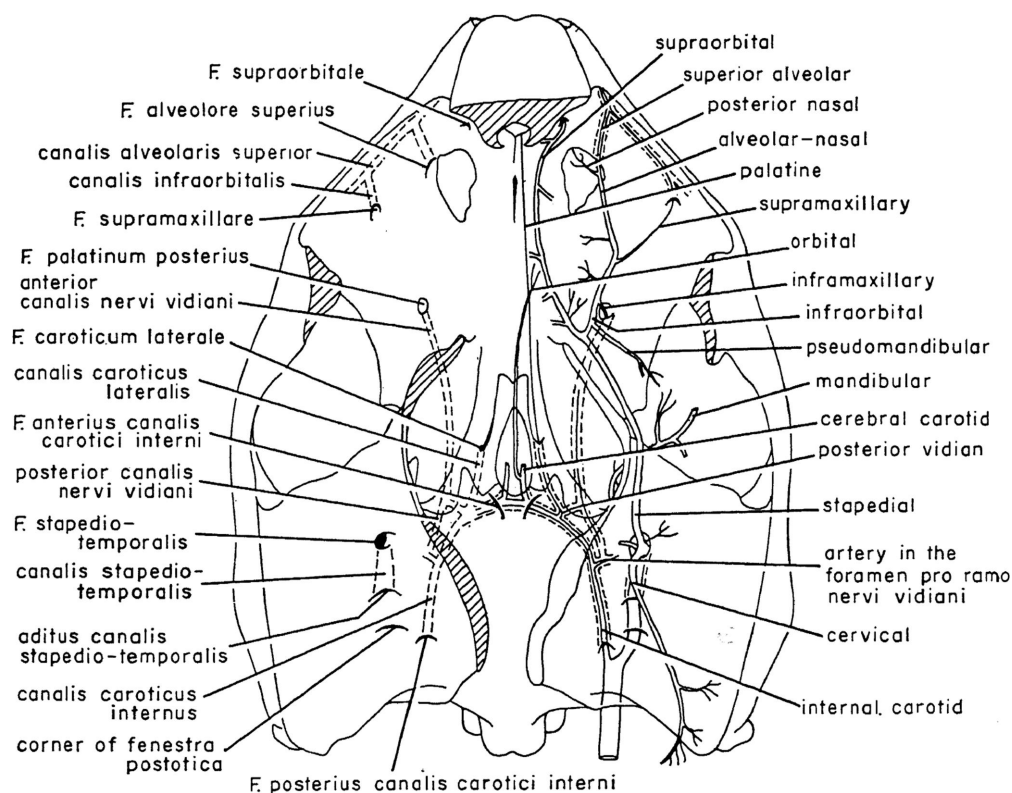


FIG. 30. Semidiagrammatic dorsal view of cranial arteries (right side), and foramina and canals (left side) in *Chrysemys scripta*, Emydidae. From Albrecht (1967).

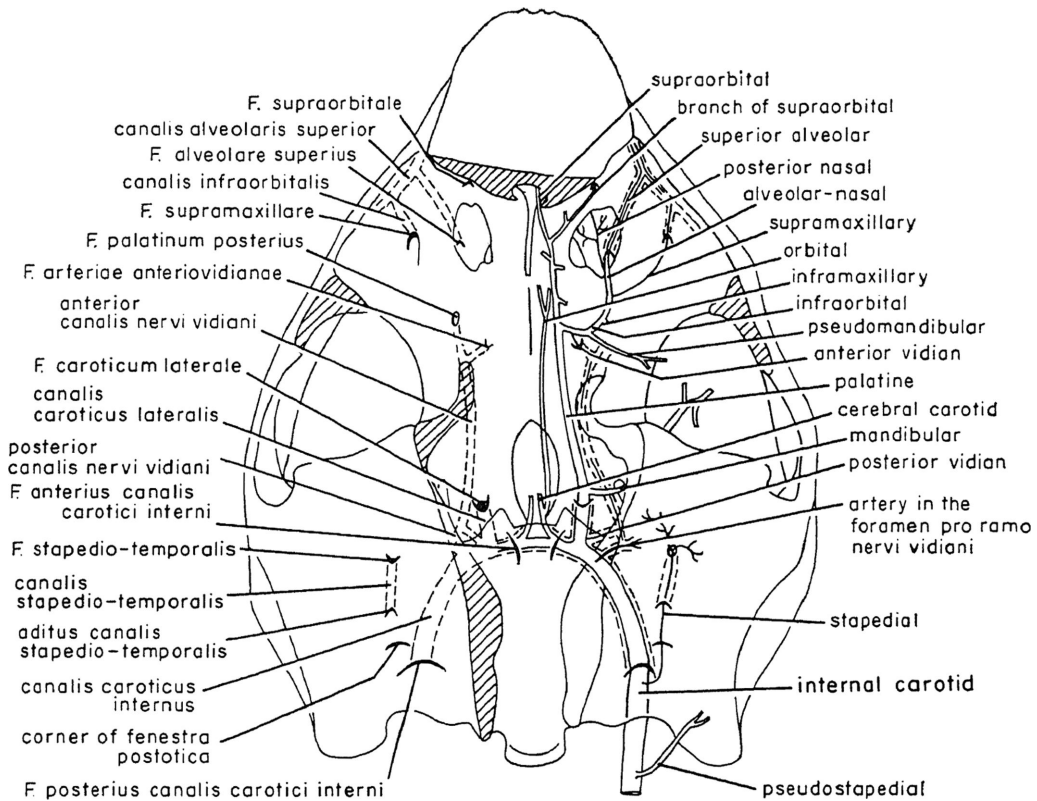


FIG. 31. Semidiagrammatic dorsal view of the cranial arteries (right side) and foramina and canals (left side) in *Sternotherus odoratus*, Kinosternidae. From Albrecht (1967).

joining the canalis cavernosus as in cryptodires, the facial nerve joins the canalis caroticus internus. The geniculate ganglion is formed at the junction of the facial nerve canal and the canalis caroticus internus. The anterior (palatine) branch of VII follows the internal carotid artery as in cryptodires but the posterior (hyomandibular) branch travels in its own canal in the prootic to enter the canalis cavernosus and continue posteriorly as in cryptodires. Therefore, the hyomandibular branch of the facial nerve is separated from the cranioquadrate space in pleurodires, whereas in cryptodires the nerve is contained in the cranioquadrate space (canalis cavernosus). Siebenrock (1897, p. 269, in

translation) also described this condition: "In the Pleurodira the nervus facialis does not enter into the canalis cavernosus immediately, as it does in the cryptodire turtles, instead it goes first into the carotid canal and from here a facialis branch goes through its own canal, posteriorly, into the canalis cavernosus, while the sympathetic [palatine] branch of the nervus facialis goes forward in the carotid canal . . ." Van der Merwe (1940, fig. 8c) gave a section of *Pelomedusa subrufa* (*P. galeata* of van der Merwe) through the ear region at the position of the geniculate ganglion. This ganglion is shown in the same space with the internal carotid artery and just dorsal to it. Sections of

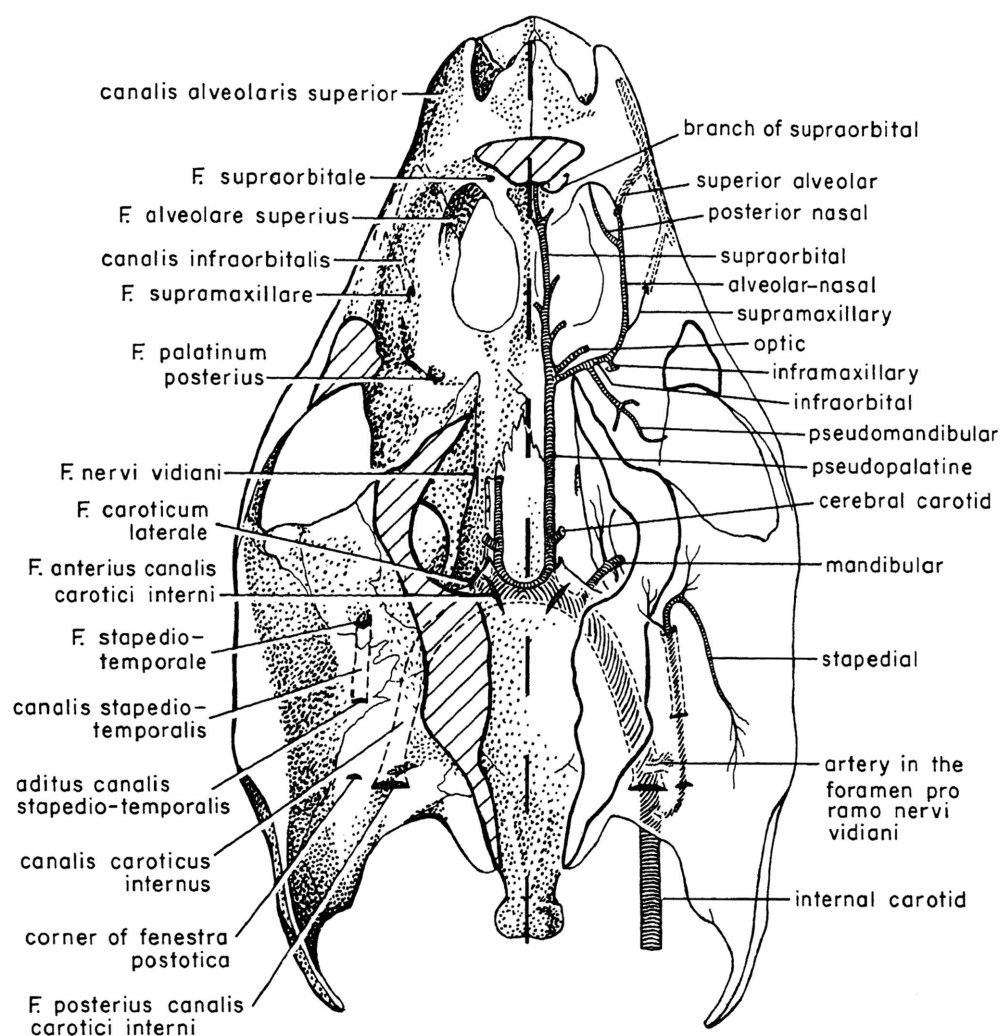


FIG. 32. Semidiagrammatic dorsal view of the cranial arteries (right side) and foramina and canals (left side) in *Trionyx spinifer*, Trionychidae. From Albrecht (1967).

Pelusios castaneus (Univ. Toronto) also show this to be the case and the above description is based mostly on these latter sections. Examinations of pleurodire skulls show some differences in this area. *Emydura macquarrii* and *E. krefftii* are essentially the same as *Pelusios* and *Pelomedusa* but the posterior or hyomandibular branch of the facial nerve (VII) never enters the canalis cavernosus and emerges beside the ca-

nalis cavernosus into the cavum acustico-jugulare. The podocnemine group shows the most diversity due to the great enlargement of the region around the canalis caroticus internus and associated changes in the position of the foramen posterior canalis carotici interni. In this group the geniculate ganglion tends to occur in a fossa in the prootic that opens ventrally into the greatly enlarged canalis caroticus inter-

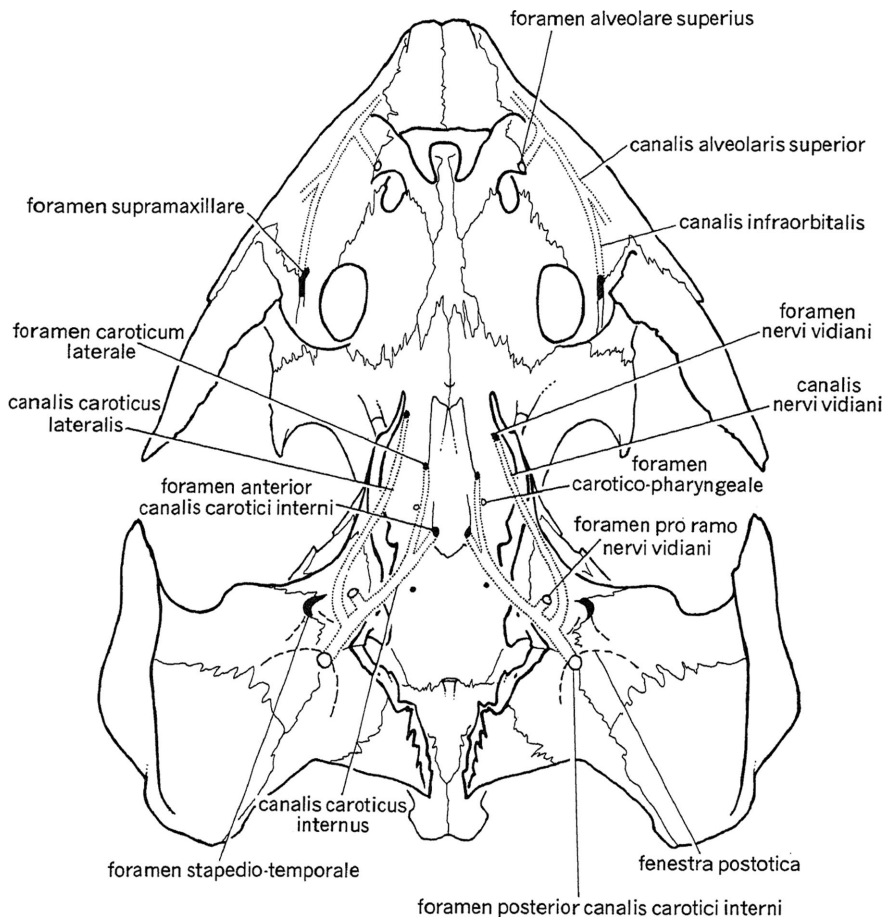


FIG. 33. Semidiagrammatic dorsal view of the cranial canals and foramina in *Chelydra serpentina*, Chelydridae. Foramina visible on dorsal surfaces shown solid; foramina hidden in dorsal view are open circles. Diameter of canals exaggerated for clarity. From Gaffney (1972b).

nus. In *Erymnochelys madagascariensis* this fossa is larger than in the other forms and the foramen for the posterior branch of the facial nerve as it enters the canalis cavernosus is much larger than in the other pleurodires. Nonetheless, in all the pleurodires I have examined the facial nerve canal communicates with the canalis caroticus internus via a fossa that apparently contains the geniculate ganglion which then sends off the posterior branch to enter the canalis cavernosus. The anterior branch goes forward in the canalis caroticus internus and,

depending on which pleurodires are examined, may utilize either the canalis nervi vidiani or the canalis caroticus lateralis (Albrecht, 1976).

The foramen pro ramo nervi vidiani is a short canal connecting the canalis cavernosus and the canalis caroticus internus. It seems to occur only in cryptodires and the reasons for this are related to the position of the facial (VII) nerve and its branches. In most reptiles the geniculate ganglion can be considered as the point of origin for the palatine branch of the facial nerve (Willard, 1915; see Soliman,

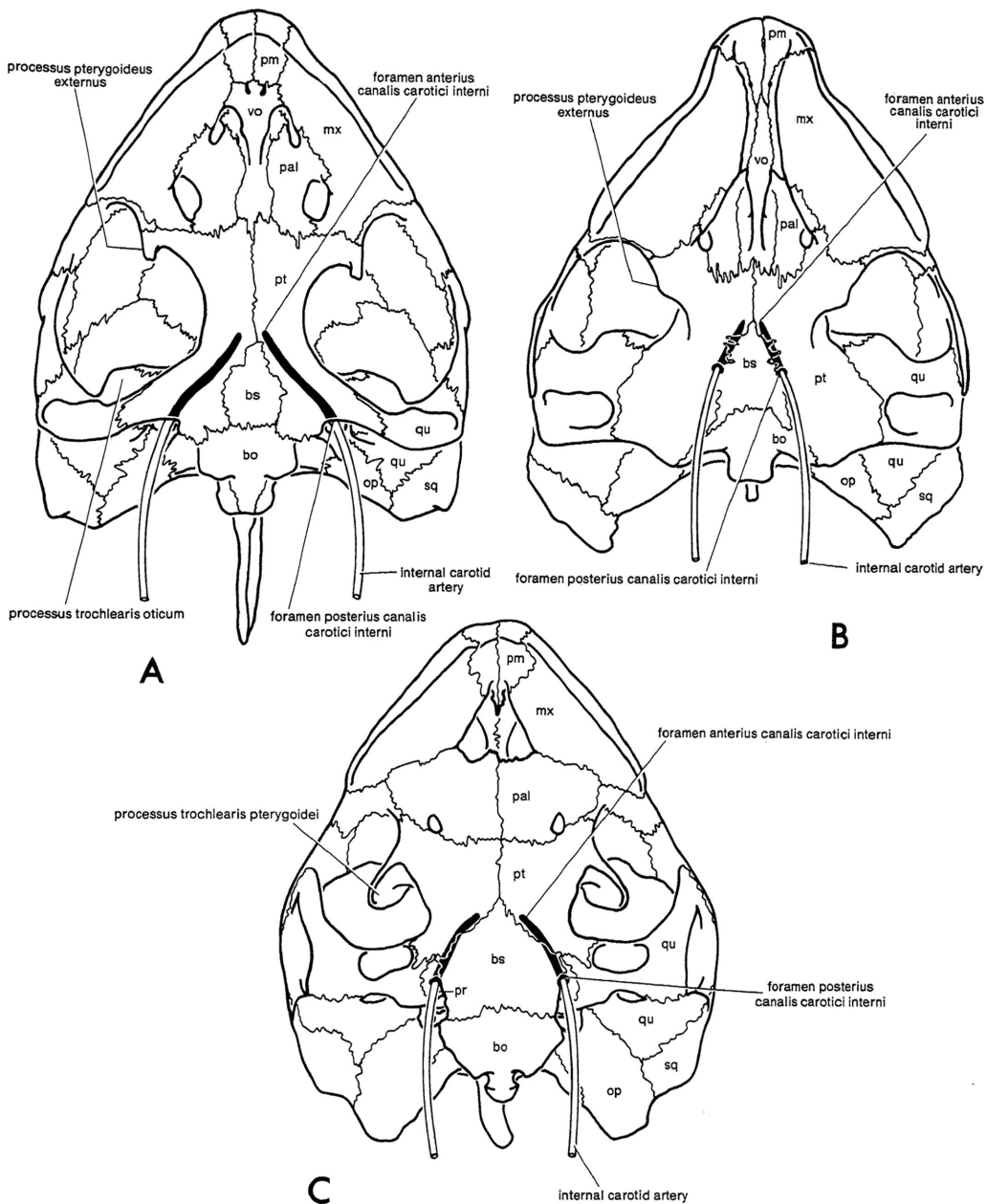


FIG. 34. Comparison of the canalis caroticus internus (in black) in three major groups of turtles: A. Eucryptodira (*Chelydra serpentina*). B. Paracryptodira (*Eubania cephalica*). C. Pleurodira (*Pelusios* sp.). The diameter of the canal is exaggerated for clarity. From Gaffney (1975d).

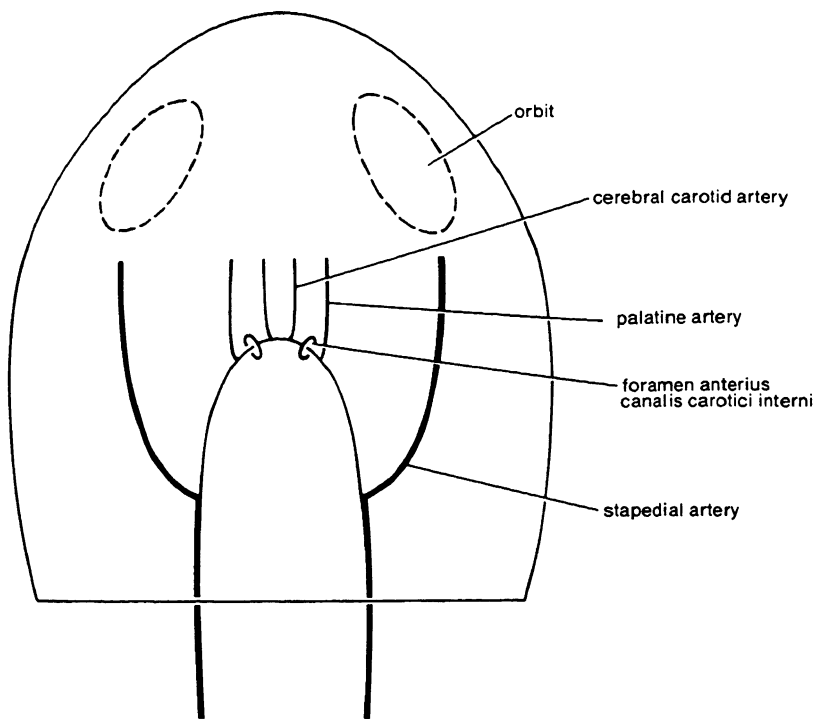


FIG. 35. Diagrammatic dorsal view of a turtle head showing relative diameters and positions of branches of the internal carotid artery. The arterial pattern shown here is suggested as the primitive condition for turtles and is repeated as A in figure 36. From Gaffney (1975d).

1964 for other references). This branch usually accompanies the internal carotid artery for a short distance, and, in cryptodires, the palatine branch must go from the geniculate ganglion (usually in the canalis cavernosus) to the canalis caroticus internus to accomplish this. The resulting canal is the foramen pro ramo nervi vidiani. In pleurodires the geniculate ganglion appears to occur consistently near or within the canalis caroticus internus and, therefore, the palatine branch does not originate in the canalis cavernosus and no foramen pro ramo nervi vidiani of the sort found in cryptodires is formed. It should be emphasized here that I have been able to examine the actual nerves in a relatively few genera and further work might result in different conclusions.

The prootic of cryptodires may form the dorsal wall of the canalis caroticus internus as

the canalis extends anteromedially into the basicranium. In many forms, such as trionychids, cheloniids, and *Macrolemys* the canalis caroticus internus may be contained within the pterygoid so that the prootic forms little or none of the canalis. In *Chelydra* and most emydids, however, the prootic forms some portion of the roof of the canalis caroticus internus.

The prootic in pleurodires is usually the main element in the formation of the foramen posterior canalis carotici interni. The ventral surface of the prootic is exposed in ventral view around the margin of the foramen posterior canalis carotici interni but the greater part of the prootic may not be exposed, especially in pelomedusids. In some cases (e.g., the right side of *Chelodina expansa*, AMNH 108948) the anterior margin of the foramen posterior canalis

carotici interni may be formed by the quadrate.

The podocnemine pleurodires have long been characterized (e.g., Boulanger, 1889, p. 189) by an unusual morphology in this area due to the invasion of the basicranium by a portion of the pterygoid musculature (see Pterygoid). The morphologic position of the foramen posterior carotici interni is conspicuously altered because it is no longer formed by the prootic in members of this group (I have not been able to see skulls of all species of *Podocnemis*). The internal carotid artery enters the skull along with the pterygoid muscle and proceeds anteromedially beneath the prootic rather than through it as in other pleurodires. There is an opening on the ventral surface of the prootic but it communicates with the facial (VII) nerve canal, here termed the foramen nervi facialis (see above for discussion). The geniculate ganglion is contained in this opening and the palatine branch of the facial nerve goes ventrally through the opening and into the enlarged "carotid" or pterygoideus channel. The palatine

branch then travels anteriorly beneath the prootic, rather than within it as in other pleurodires, to enter the canalis nervi vidiani (Albrecht, 1976).

The foramen nervi trigemini is usually formed by the prootic posteriorly and posterodorsally, the parietal dorsally (and anteriorly in some cases), the epipterygoid anteriorly (when present), and the pterygoid ventrally. The maxillary (V_2) and mandibular (V_3) branches of the trigeminal (V) nerve leave the skull via this opening. In most cryptodires the mandibular artery (arteria mandibularis, Albrecht, 1967, 1976) also leaves via the foramen nervi trigemini, whereas in pleurodires the mandibular artery branches off the stapedial artery after the latter exits from the foramen stapedio-temporale. In some cryptodires the foramen nervi trigemini may be subdivided so that the various soft structures are separated by bone as reported by Siebenrock (1897, figs. 6, 9) in *Geoemyda spinosa* (*Heosemys spinosa* of McDowell, 1964) and *Cyclemys dentata*

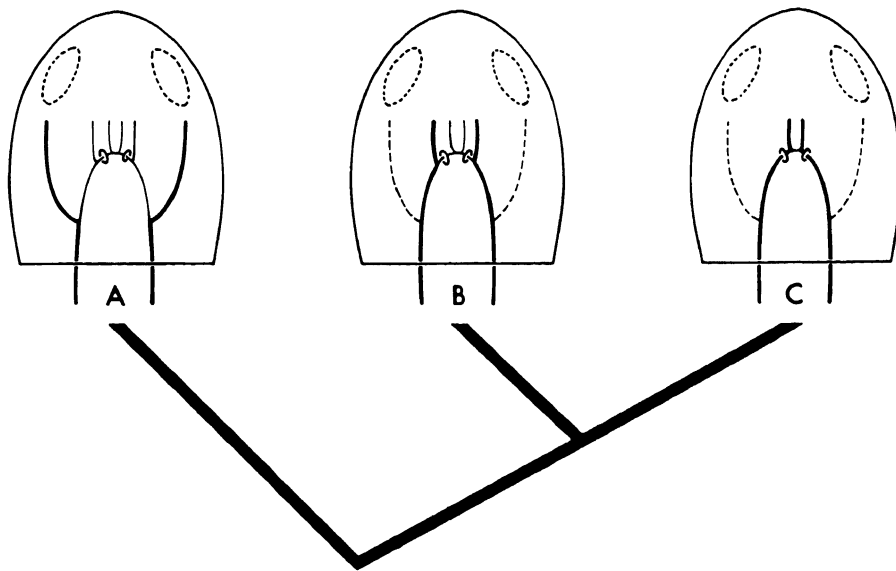


FIG. 36. A cladogram showing the relationships of trionychoid turtles based on arterial patterns in the head. A. Primitive condition for turtles. B. Pattern found in the Kinosternidae and Dermatemnydidae. C. Pattern found in the Carettochelyidae and Trionychidae. See figure 35 for identification of arteries. From Gaffney (1975d).

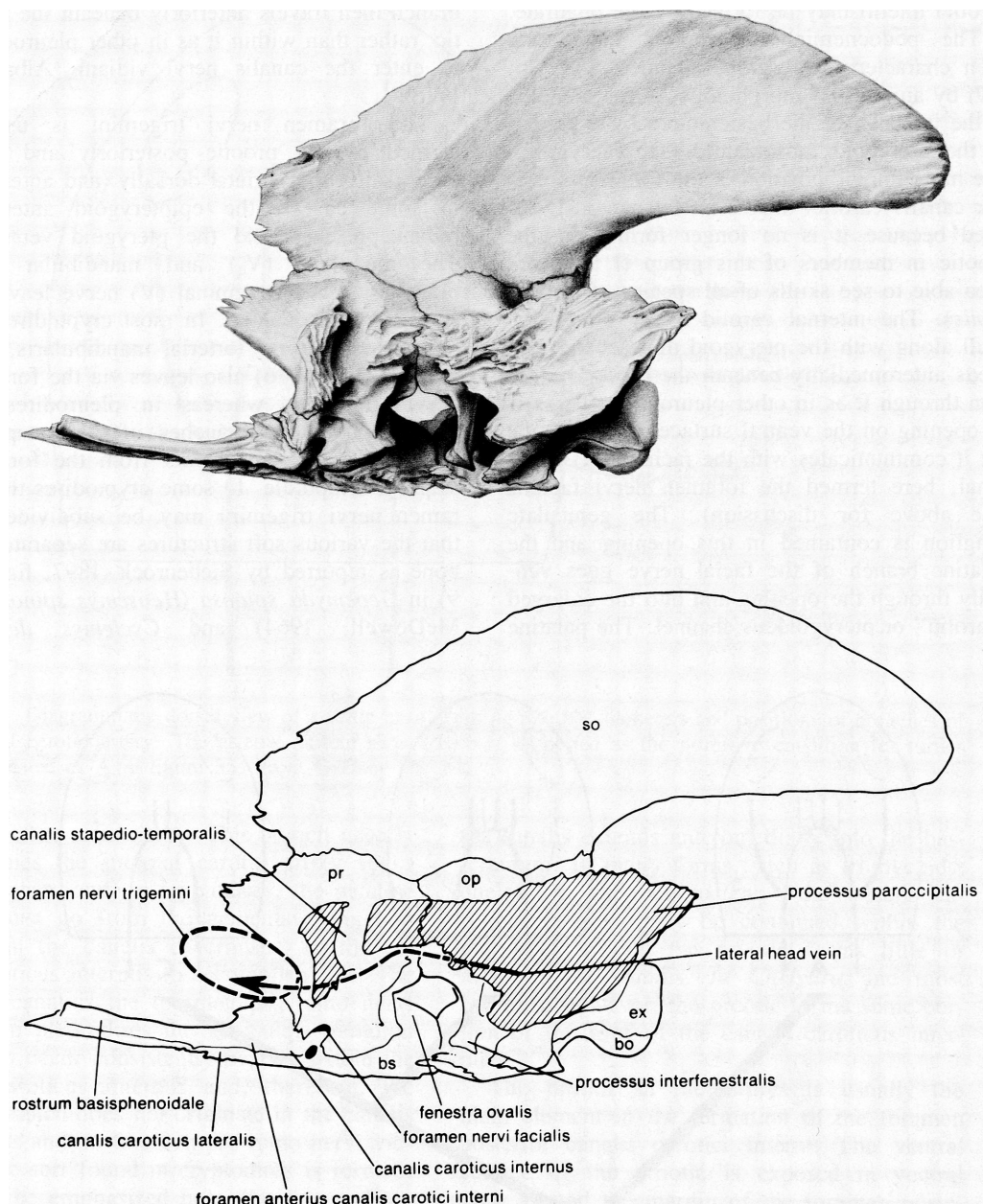


FIG. 37. *Chelydra serpentina* (AMNH 107387), Chelydridae, no data. Lateral view of the primary neurocranium in a cryptodire. Hatching indicates sutural contact with palatoquadrate elements above remnant of cranioquadrate space. Anterior is to the left. See figure 38. From Gaffney (1975d).

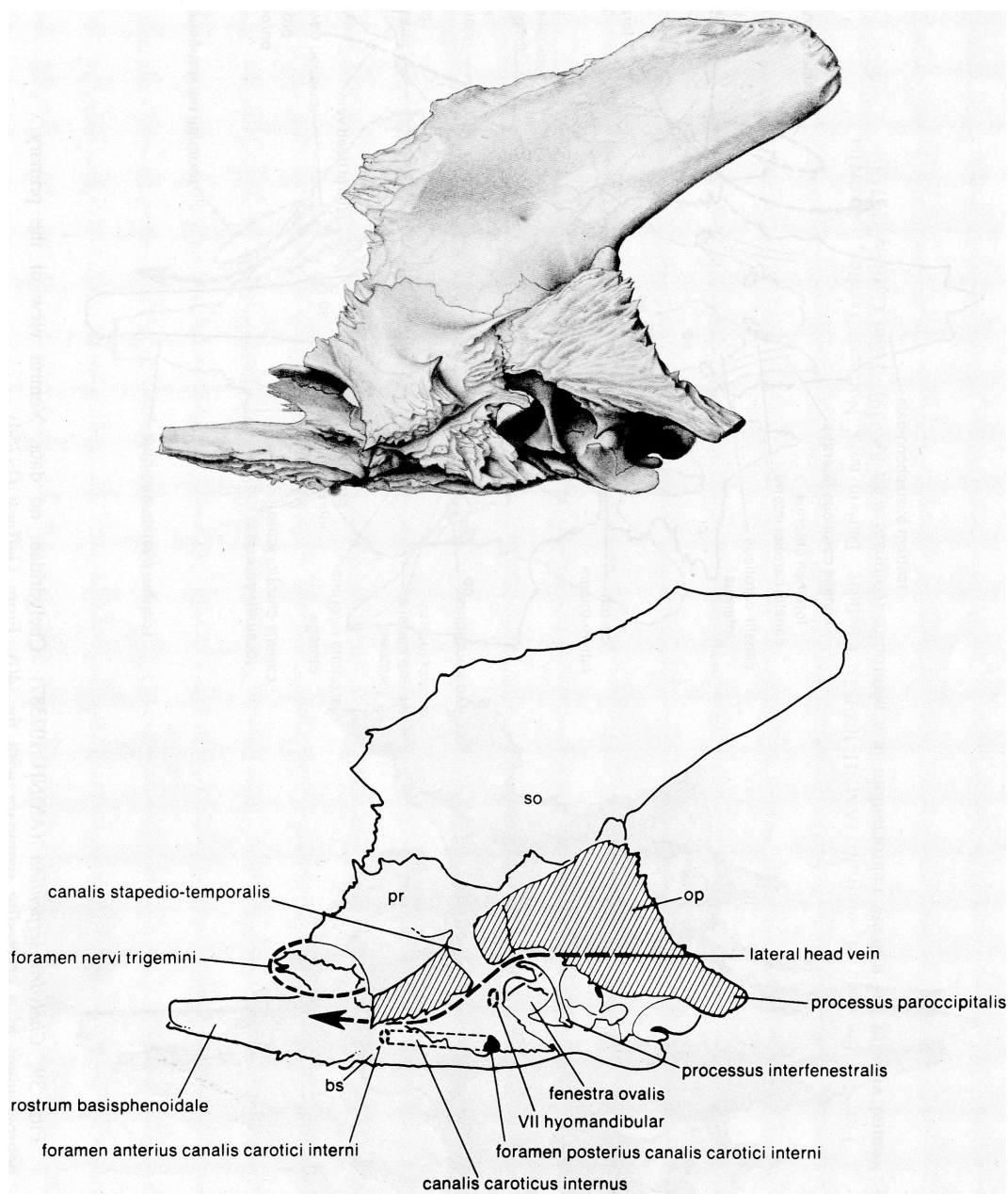


FIG. 38. *Emydura cf. australis* (AMNH 108957), Chelidae, Darwin area, Northern Territory, Australia. Lateral view of the primary neurocranium in a pleurodire. Hatching indicates sutural contact with palatoquadrate elements above remnants of cranio-quadrate space. Anterior is to the left. See figure 37. From Gaffney (1975d).

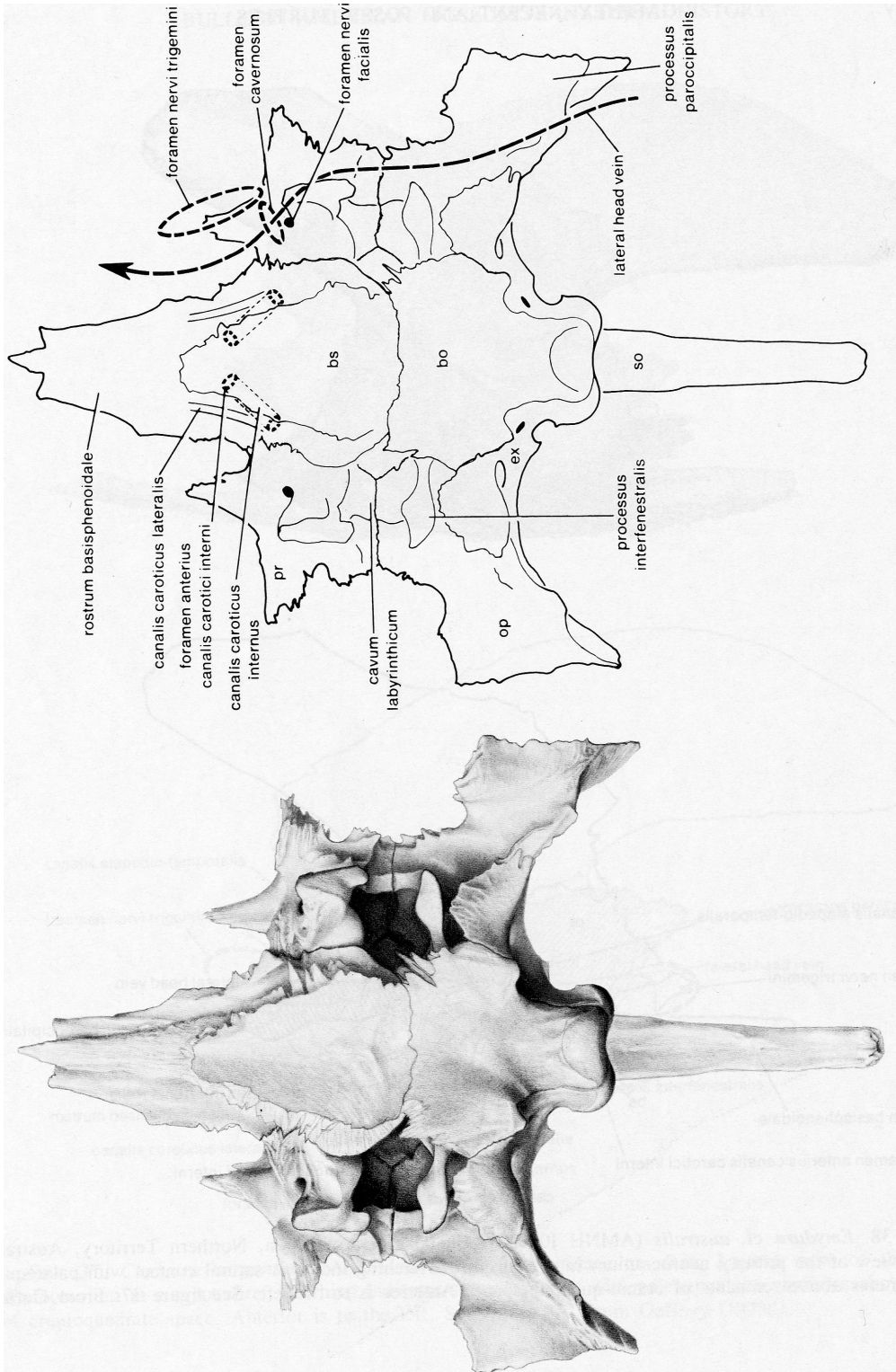


FIG. 39. *Chelydra serpentina* (AMNH 107387), Chelydridae, no data. Ventral view of the primary neurocranium in a cryptodire (compare with fig. 40). From Gaffney (1975d).

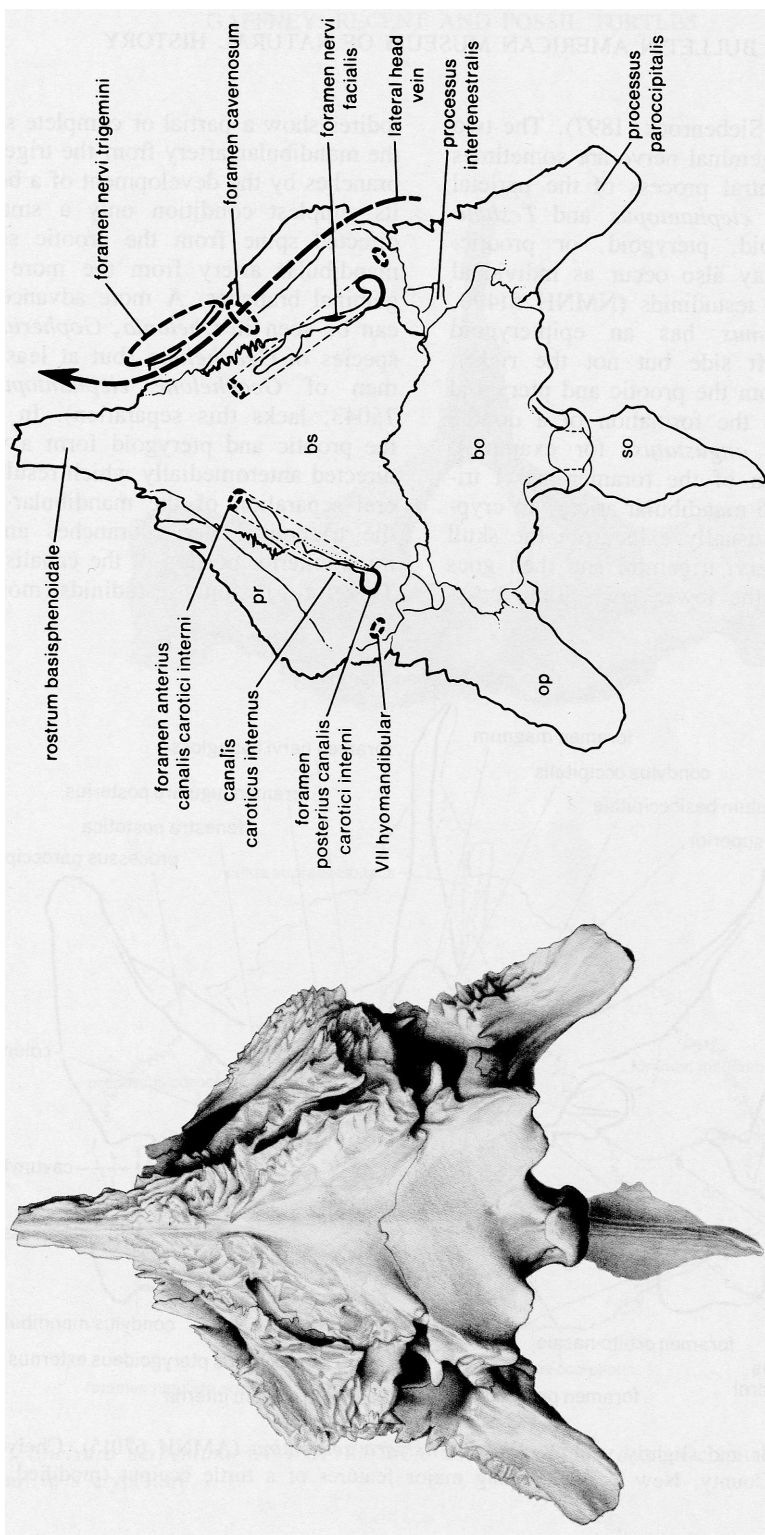


FIG. 40. *Emydura cf. australis* (AMNH 108957), Chelidae, Darwin area, Northern Territory, Australia. Ventral view of the primary neurocranium in a pleurodire (compare with fig. 39). From Gaffney (1975d).

(*Cyclemys dhor* of Siebenrock, 1897). The two branches of the trigeminal nerve are sometimes separated by a ventral process of the parietal (as in *Geochelone elephantopus* and *Testudo graeca*) epipterygoid, pterygoid, or prootic. These processes may also occur as individual variations in some testudinids (NMNH 51490, *Gopherus polyphemus* has an epipterygoid process on the left side but not the right). Small processes from the prootic and pterygoid may also result in the formation of a double foramen (*Claudius angustatus*, for example). Another subdivision of the foramen nervi trigemini involves the mandibular artery. In cryptodires this artery usually exits from the skull via the foramen nervi trigemini and then goes anteroventrally to the lower jaw. Some cryp-

todires show a partial or complete separation of the mandibular artery from the trigeminal nerve branches by the development of a bony wall. In its simplest condition only a small ventrally directed spine from the prootic separates the mandibular artery from the more medial trigeminal branches. A more advanced condition can be seen in *Chelonia*, *Gopherus*, and most species of *Geochelone* (but at least one specimen of *Geochelone elephantopus*, AMNH 75043, lacks this separation). In these forms the prootic and pterygoid form a vertical wall directed anteromedially which results in the lateral separation of the mandibular artery from the trigeminal nerve branches and from the more anterior portion of the canalis cavernosus. Therefore, in some testudinids (most specimens

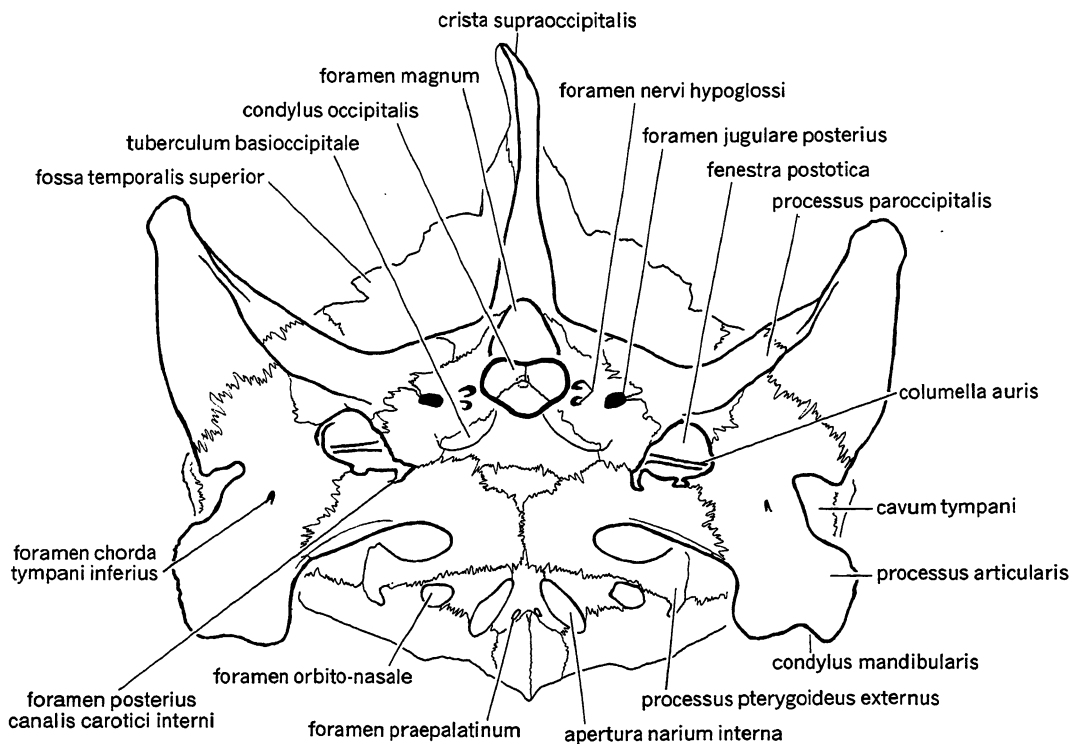


FIG. 41. Posterior and slightly ventral view of *Chelydra serpentina* (AMNH 67015), Chelydridae, Bronxville, Westchester County, New York, showing major features of a turtle occiput (modified from Gaffney, 1972b).

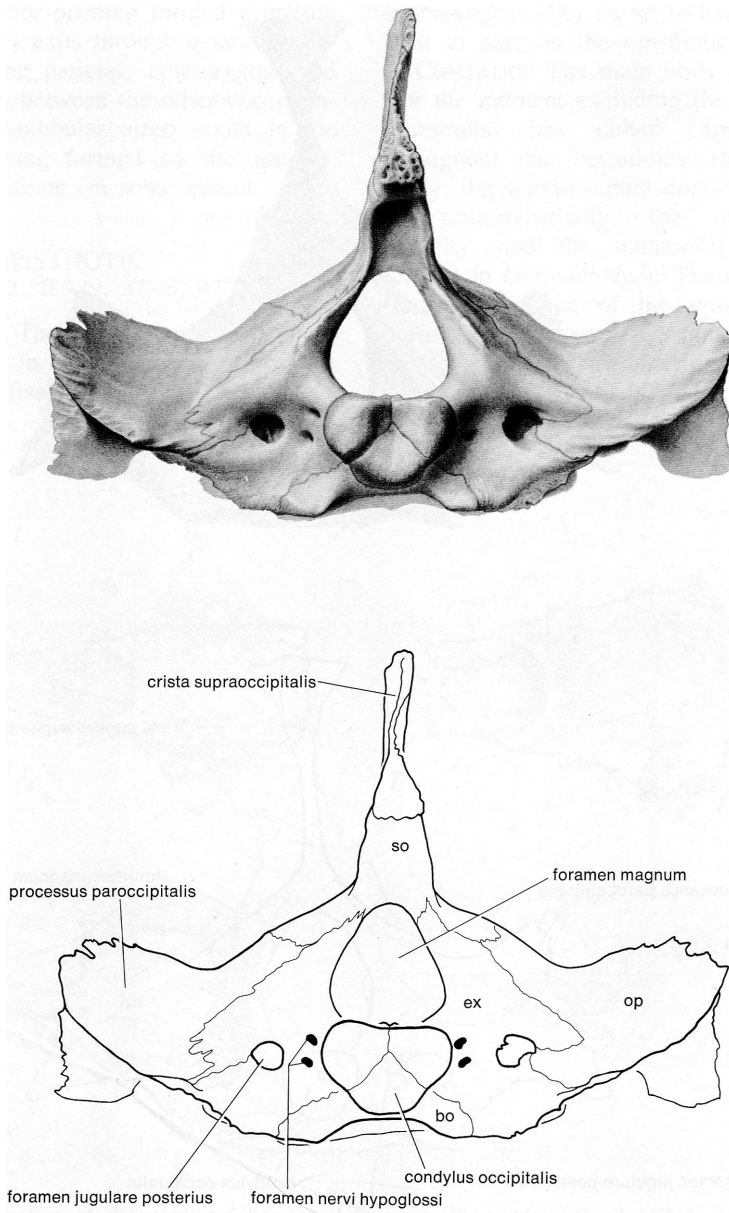


FIG. 42. *Chelydra serpentina* (AMNH 107387), Chelydridae, no data. Occipital view of the primary neurocranium in a cryptodire.

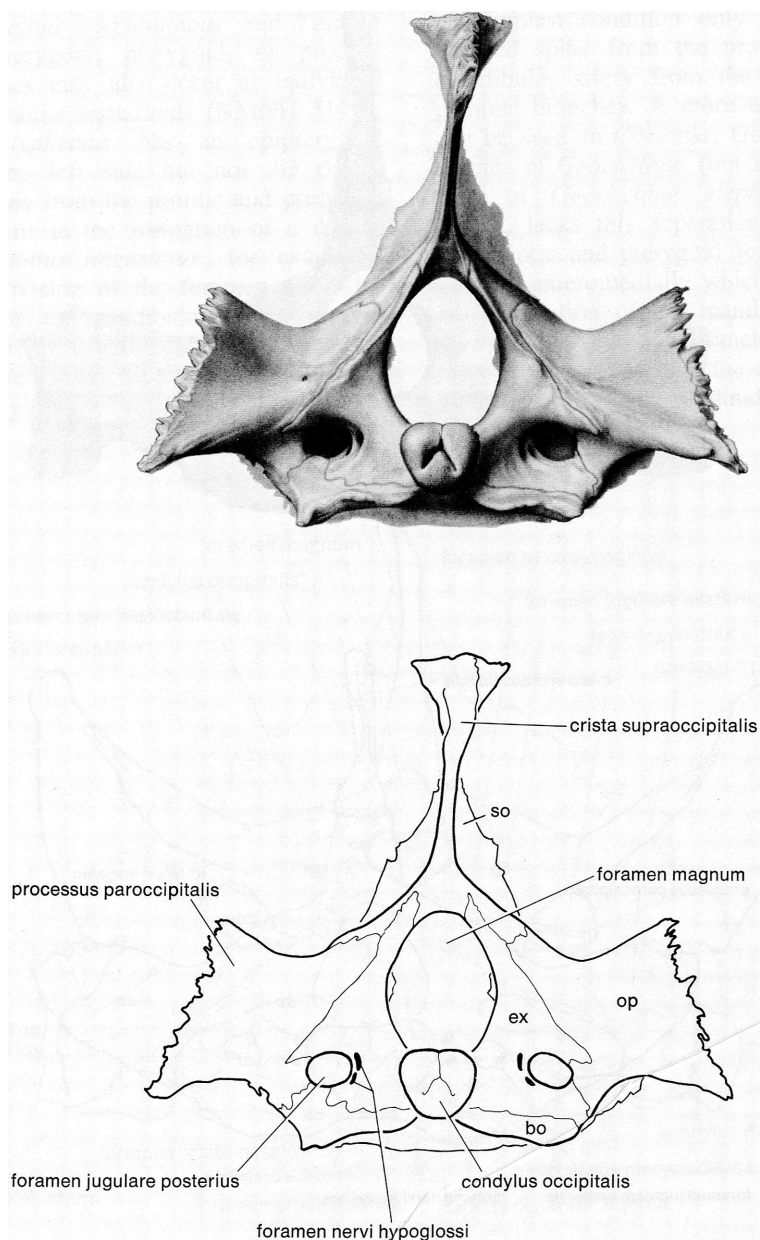


FIG. 43. *Emydura cf. australis* (AMNH 108957), Chelidae, Darwin area, Northern Territory, Australia. Occipital view of the primary neurocranium in a pleurodire.

of *Geochelone elephantopus*, for example) each of the three main trigeminal structures may emerge from the skull in its own foramen: V_2 has a small, anterior opening formed primarily by the parietal; V_3 exits through a large opening formed by the parietal, epipterygoid and prootic which lies between the other two openings; and the mandibular artery exits in the most lateral opening formed by the prootic, pterygoid and quadrate (in some cases).

OPISTHOTIC

Figures 11, 12, 18, 19, 37-43, 47-102

DEVELOPMENT: The opisthotic is a cartilage bone that ossifies in the posterior half of the otic capsule. The fissura metotica is equivalent

to the foramen jugulare anterius of the adult skull and has its anterior margin formed by the opisthotic ossification. The path of the glosso-pharyngeal (IX) nerve is usually ossified, at least in part, in the opisthotic.

CONTACTS: The main body of the opisthotic (for the moment excluding the processus interfenestralis) has rather consistent contacts throughout the Testudines: the prootic anteriorly, the supraoccipital dorsally, the exoccipital posteromedially, the quadrate anterolaterally, and the squamosal posterolaterally (except in *Dermochelys*). There may be a ventromedial contact of the opisthotic with the basioccipital between the hiatus acusticus and the foramen jugulare anterius but often this is prevented due to lack of ossification (as in most

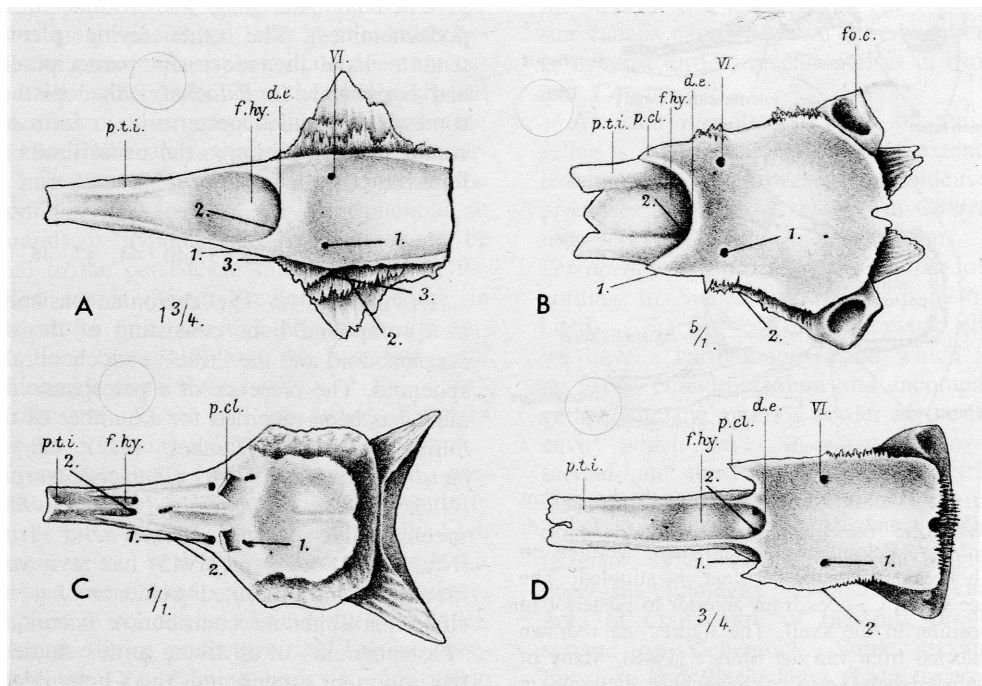


FIG. 44. Dorsal views of disarticulated basisphenoids, anterior to the left. A. *Chelodina longicollis*. B. *Sternotherus odoratus*. C. *Chelonia mydas*. D. *Macrolemys temminckii*.

Abbreviations: d.e., dorsum sellae; f. hy., sella turcica; fo. c., floor of the cavum labyrinthicum; p. cl., processus clinoideus; p.t.i., rostrum basisphenoidale; 1.-1, canalis nervi abducentis; 2.-2, canalis caroticus internus; 3.-3, canalis nervi vidiani; VI, foramen nervi abducentis. From Siebenrock (1897).

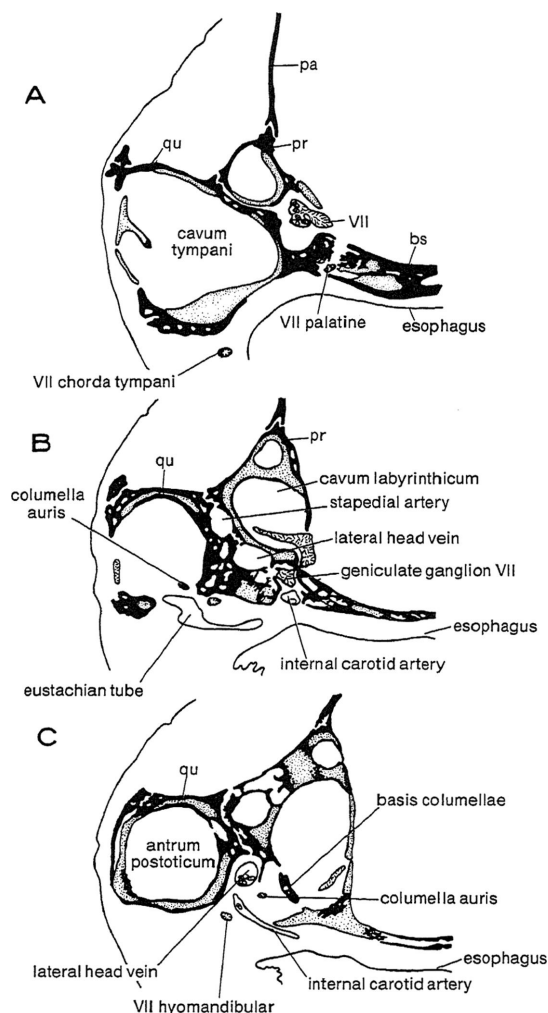


FIG. 45. Transverse sections through the cavum labyrinthicum and associated structures of *Pelomedusa galeata*, Pelomedusidae, no data. Midline on right, bone is in black, cartilage is stippled. The sequence A, B, C, goes from anterior to posterior in their position in the skull. The figures are redrawn and relabeled from van der Merwe (1940). Many of the original labels seem to have been in error in view of my study of sectioned heads of *Pelusios* and other pelomedusids.

pleurodires) or an extension of the exoccipital (as in *Chelonia*). In most cases the processus interfenestralis ends in cartilage but when com-

pletely ossified it usually articulates with the pterygoid and basioccipital in cryptodires and with the prootic and basioccipital in pleurodires.

STRUCTURES: The opisthotic (figs. 49, 105, 109) may be divided into two portions: an anteromedial region containing part of the cavum labyrinthicum and a posterolateral region roofing some of the cavum acustico-jugulare and forming the processus paroccipitalis. Because most of the opisthotic is involved in the formation of the cavum labyrinthicum and the cavum acustico-jugulare most features of the opisthotic are discussed under those headings.

The processus paroccipitalis extends posterolaterally from the cavum labyrinthicum portion of the opisthotic to the squamosal. The processus is quite variable in morphology throughout the turtles, being short and stubby in *Chelonia* and long and rodlike in living podocnemines. The other living pleurodires tend to have the processus paroccipitalis flat and horizontal. In *Pelochelys* the opisthotic is somewhat extended posteriorly to form a horizontal sheet posterior to the usual limits of the fenestra postotica.

BASISPHENOID

Figures 9, 18, 30-33, 37-40, 44, 47, 48, 53-83

DEVELOPMENT: The chelonian basisphenoid is a compound bone consisting of the dermal parasphenoid and the "true" endochondral basisphenoid. The presence of a parasphenoid rudiment has been recorded for a number of turtles: *Emys orbicularis* (Kunkel, 1912); *Chrysemys picta* (Shaner, 1926); *Chelydra serpentina* (Nick, 1912); *Podocnemis* (Gaupp, 1905, no species given); and *Dermochelys coriacea* (Nick, 1912). Pehrson (1945) has reviewed this literature and presented evidence that an ossified parasphenoid contribution occurs in the "basisphenoid" of all living turtles studied with the important exception of the Cheloniidae. According to Pehrson, most turtles have (as do most vertebrates) an anterior and a posterior parasphenoid blastema in front of and behind the fenestra hypophyseos. The anterior parasphenoid blastema degenerates but the posterior one eventually floors the fenestra hypophyseos

(the sella turcica of the adult) and ossifies as part of the basisphenoid. In cheloniids, however, the posterior parasphenoid blastema is also transitory (if present) and does not ossify in the adult. Instead the rostrum basisphenoidale of cheloniids ossifies from a structure, the taenia intertrabecularis of Pehrson. This structure is a sagittal bar that runs from the trabecula communis to the crista sellaris (dorsum sellae of the adult) and divides the fenestra hypophyseos (sella turcica of the adult) in half. This helps explain the considerable morphologic difference between the rostrum basisphenoidale and sella turcica of cheloniids and other turtles. *Dermochelys* is the only other turtle known to have a taenia intertrabecularis developed in the embryo but in this form the posterior parasphenoid blastema does ossify, whereas the taenia does not. Nonetheless, it would appear that the condition in *Dermochelys* is even more specialized than in cheloniids because the rostrum basisphenoidale does not ossify at all in the adult. Thus the cheloniids and *Dermochelys* share a specialized feature, the taenia intertrabecularis that divides the sella turcica into two halves but ossifies only in the cheloniids. The loss of the parasphenoid in cheloniids is hypothesized by Pehrson to be related to the persistence into the adult of the ossified taenia intertrabecularis, whereas in *Dermochelys* this, although present in the embryo, does not ossify and the posterior parasphenoid blastema does ossify.

CONTACTS: As far as I am aware all turtles have the following contacts of the basisphenoid: anterolaterally with the pterygoid, dorsolaterally with the prootic, and posteriorly with the basioccipital. Pleurodires usually have a lateral contact with the quadrate although this may be quite limited or absent. The quadrate-basisphenoid contact is particularly well developed in the living podocnemines. The basisphenoid reaches the palatine bones in this group and in the trionychids, whereas in *Pelochelys* it also contacts the vomer (Siebenrock, 1897). In *Chelus* the basisphenoid has a limited posterior contact with the exoccipital.

STRUCTURES: The basisphenoid (figs. 44, 104) has its most complex morphology on its

dorsal surface. The sella turcica and dorsum sellae are easily identified and used as morphologic landmarks. The sella turcica is a pit or depression housing the pituitary in the center of the basisphenoid with the raised dorsum sellae forming its posterior wall. The sella turcica may be a fairly open, shallow depression, as in *Chelydra*, or it may be a deep pit, open only at the top, as in *Eseya*. The shape of the sella turcica may also vary from being broad and oval as in *Geochelone* (*sensu* Loveridge and Williams, 1957) to long and narrow, as in *Malaclemys*. Living cheloniids have a nearly obliterated sella turcica and differ from all other turtles in this respect (see preceding development section). In all turtles the internal carotid arteries enter the sella turcica via the paired foramen anterior canalis carotici interni. Each foramen usually enters the skull just medial to the base of each trabeculum. The foramen anterior canalis carotici interni may be quite small, as in most turtles, or enlarged as in trionychids and *Carettochelys*.

At each dorsolateral edge of the dorsum sellae is a paired process usually extending anterodorsally, the processus clinoides. These processes are least developed in *Chelydra* and most chelids, while in some forms, such as *Terrapene*, the processes are quite long. According to Siebenrock (1897, p. 216, translated)—“Starting at the processus clinoides we have a cartilaginous band which stretches up to the chondrocranium and encompasses together with the anterior border of the prootic a cavity which serves as a passageway for the second and third branches of the trigeminal nerve.” The cartilaginous band is the pila prootica of the fully developed chondrocranium (Kunkel, 1912). The variation in length of the processus clinoides presumably reflects the degree of ossification of the pila prootica described by Siebenrock. Some specimens of *Emydura* and *Plesiochelys* (Late Jurassic) seem to have nearly all of this band ossified.

The abducens (VI) nerve pierces the basisphenoid by going through the base of the processus clinoides via the canalis nervi abducentis. The posterior foramen nervi abducentis is on the dorsal surface of the basisphenoid

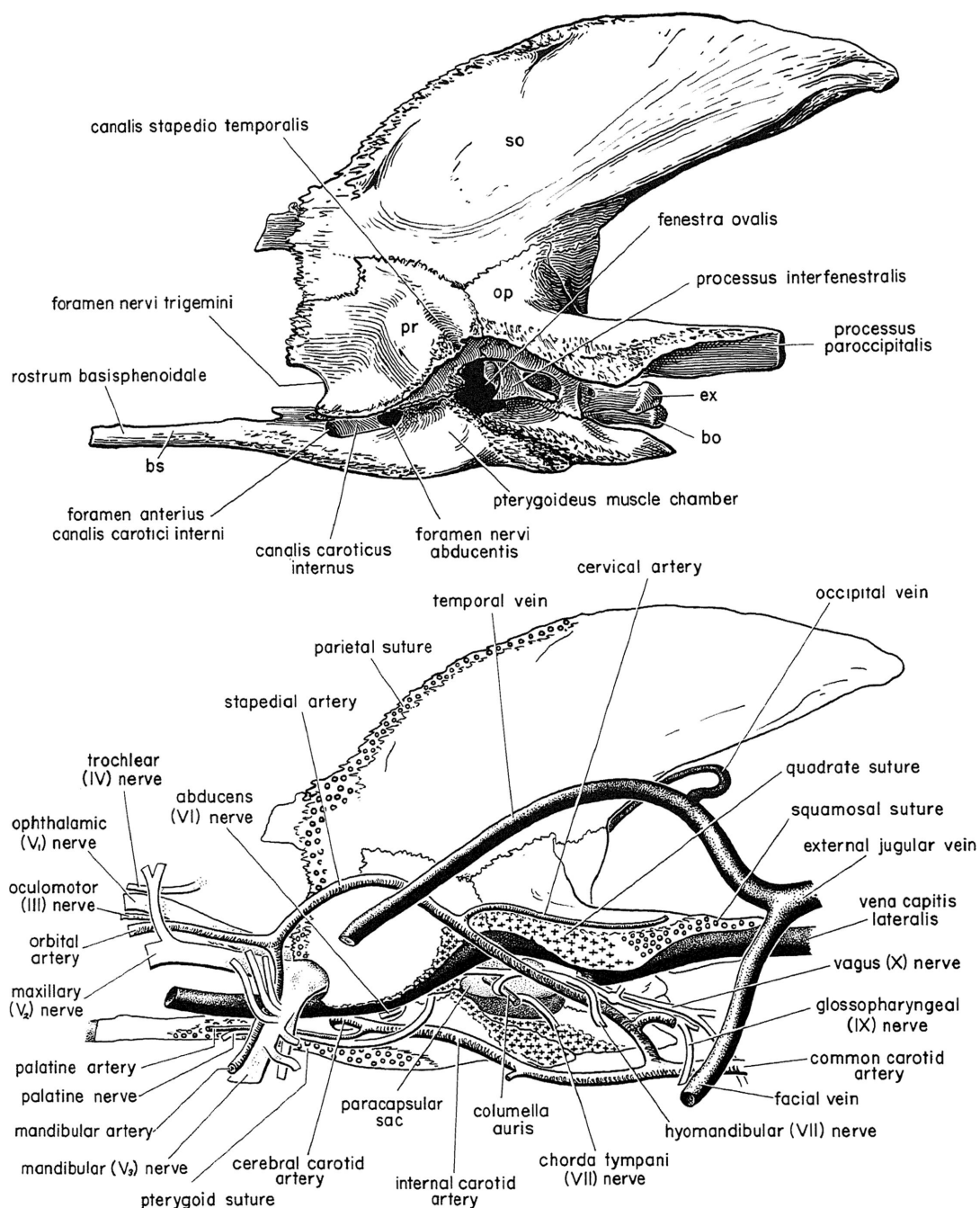


FIG. 46A. *Podocnemis expansa*, Pelomedusidae, no data. Lateral view of the primary neurocranium showing arteries, veins, and nerves. Bones are from an adult, and soft structures are from a juvenile. Note that this genus is characterized by specializations in the carotid canal and mandibular artery, and these structures should not be considered typical for turtles. I am indebted to Dr. S. B. McDowell for these figures and the identifications.

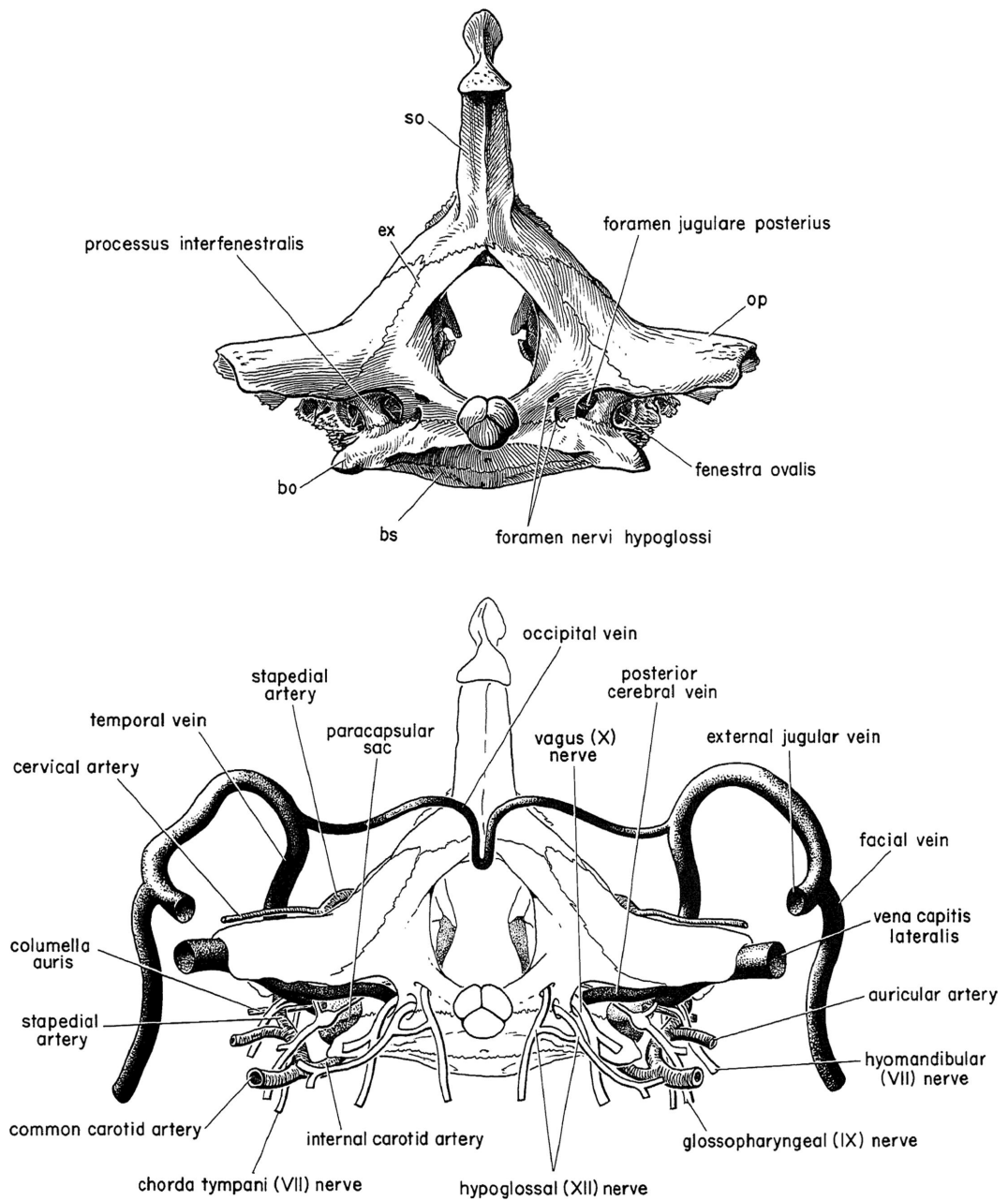


FIG. 46B. *Podocnemis expansa*, Pelomedusidae, no data. Occipital view of the primary neurocranium showing arteries, veins, and nerves. See caption for figure 46A. I am indebted to Dr. S. B. McDowell for these figures and the identifications.

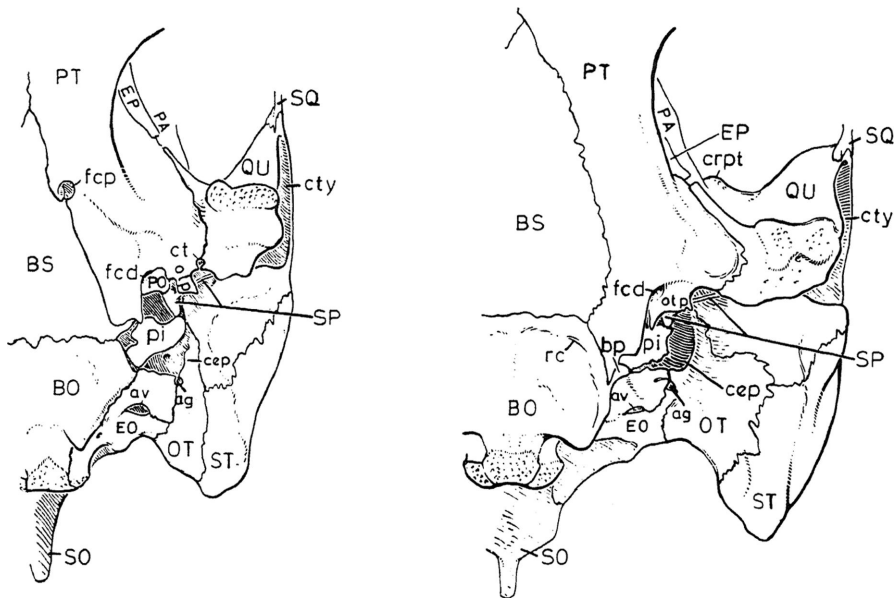


FIG. 47. Ventral views of the left basicranial region in *Clemmys guttata* (left), Emydidae; and *Mauremys caspica* (right), Emydidae (*Clemmys caspica* of Wermuth and Mertens, 1961). This figure shows some of the features used by McDowell (1964) to differentiate the Emydinae (*Clemmys*) from the Batagurinae (*Mauremys*). In particular, the large foramen caroticopharyngeale (fcp) in *Clemmys* and its absence in *Mauremys*; the posterior extension of the pterygoid in *Mauremys*; and the "batagurine process" on the basioccipital in *Mauremys*. I am indebted to Dr. McDowell for these figures.

Abbreviations: (McDowell's names are in parentheses where they differ from mine). ag, (apertura glossopharyngei); atEO, attachment for exoccipital; atOT, attachment for opisthotic; av, foramen jugulare posterius (apertura vagi); BO, basioccipital; bp, batagurine process; BS, basisphenoid; cep, (crista exoparacapsularis); crpt, processus trochlearis oticum (crista praetemporalis); ct, foramen chorda tympani inferius; cty, cavum tympani; EO, exoccipital; EP, epipterygoid; fcd, foramen posterius canalis carotici interni (foramen caroticum definitivum); fcp, foramen caroticopharyngeale; feg, foramen externum nervi glossopharyngei; fig, foramen internum nervi glossopharyngei (foramen internum glossopharyngealis); fp, fenestra perilymphatica; OT, opisthotic; otp, process of pterygoid bearing the medial end of the operculum tubae; PA, parietal; ph, hiatus postlagenum (postlagena hiatus); pi, processus interfenestralis; PO, prootic; PT, pterygoid; QU, quadrate; rc, rectus capitis muscle scar; rst, recessus scalae tympani; SO, supraoccipital; SP, columella auris; SQ, quadrato-jugal (squamosal); ST, squamosal (supratemporal). From McDowell (1964).

posterior to the processus clinoides and just medial to the prootic-basisphenoid suture. The surface of the basisphenoid at this point is usually tilted posteriorly so that the canalis nervi abducentis, which is nearly horizontal, penetrates the basisphenoid at an angle. The anterior foramen nervi abducentis usually occurs just lateral to the base of the processus clinoides and medial to the canalis cavernosus.

Podocnemis expansa has an unusual condi-

tion of the canalis abducentis. The extreme enlargement of the canalis caroticus internus (see Pterygoid) has caused the partial union of the canalis caroticus internus and the canalis nervi abducentis. In some specimens (AMNH 97124) both anterior and posterior foramina nervi abducentis are considerably enlarged and the canalis nervi abducentis is completely absent.

The posterior half of the basisphenoid is usually concave dorsally and comparatively free

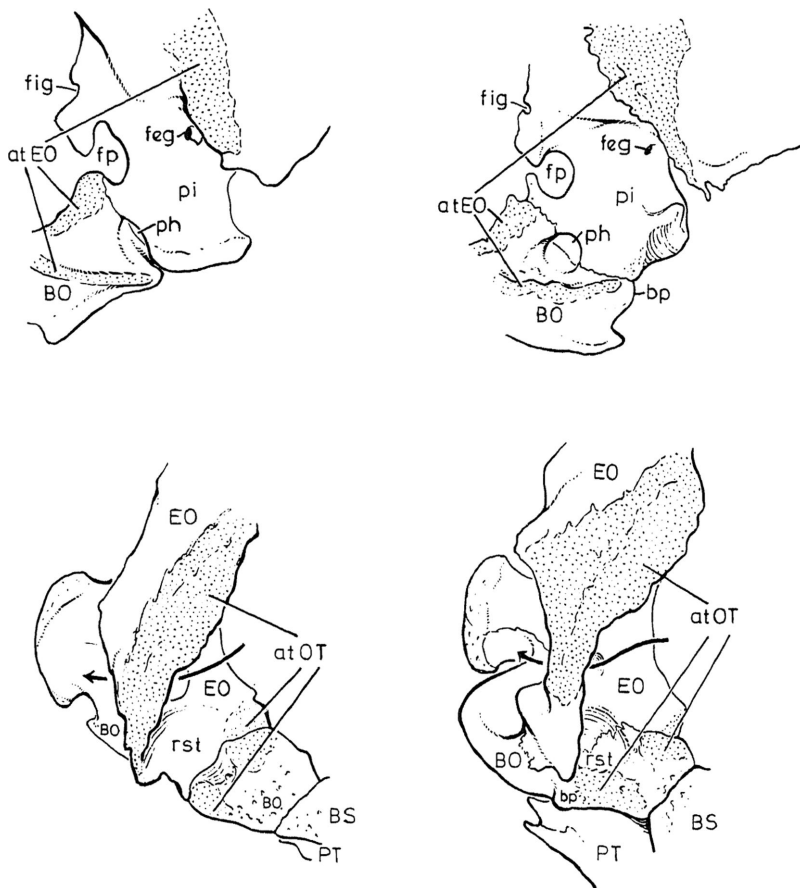


FIG. 48. The recessus scalae tympani of *Clemmys guttata* (left) and *Mauremys* (*Clemmys* of Wermuth and Mertens, 1961) *caspica* (right). The upper row shows the anterior wall of the recessus, as viewed from directly behind after removal of the exoccipital; the lower row shows the posterior, medial, and ventral walls in three-quarter view after removal of the opisthotic. Arrow indicates course of the vagus (X) nerve. From McDowell (1964). See figure 47 for abbreviations.

of structures. A slight median ridge may be developed but this seems to vary within a species. A small raised tubercle that may occur on the basisphenoid-basioccipital suture, the basis tuberculi basalis is quite well developed on the basisphenoid in cheloniids and some emyids (see Basioccipital).

The anterior half of the dorsal surface is dominated by the rostrum basisphenoidale. This is the ossification of the embryonic trabeculae (see preceding development section) and the

morphology of the rostrum basisphenoidale depends to a considerable extent on the degree of ossification of the trabeculae. In adult forms, however, the degree of trabecular ossification seems to be consistent within most species. For example, in trionychids and baenids the rostrum itself is greatly reduced and consists only of the posterolateral portion of the trabeculae. In most testudinoids the trabeculae meet in the midline forming a complete depression for the sella turcica. Many pleurodires possess a very

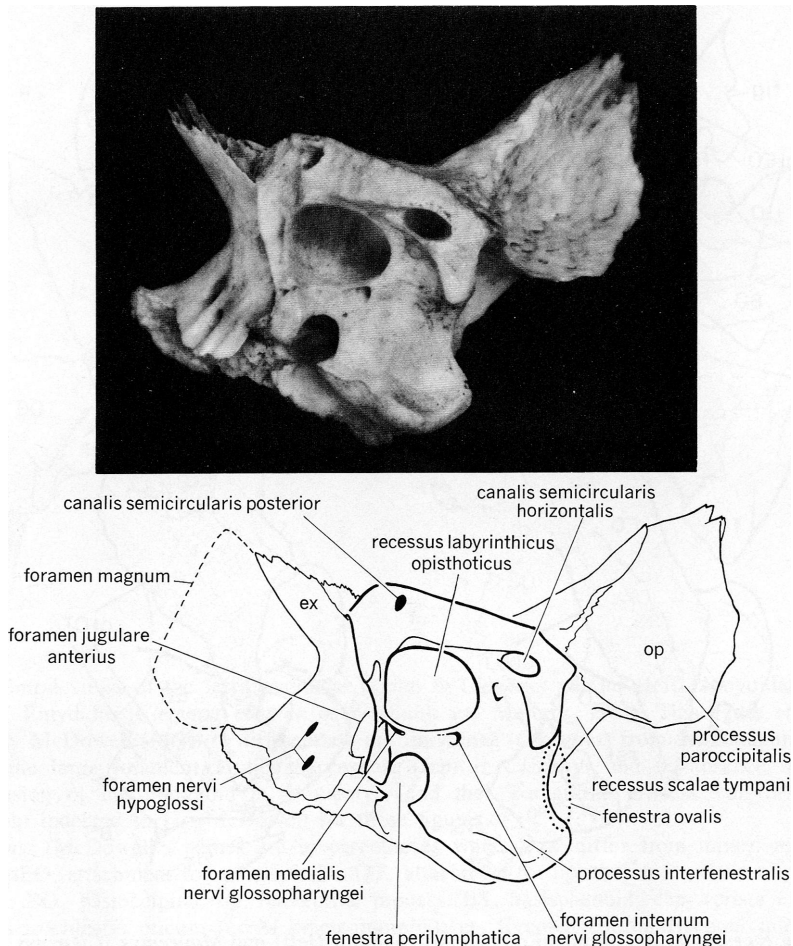


FIG. 49. Posterior and slightly medial view of left opisthotic and exoccipital exposing posterior half of cavum labyrinthicum in *Chelydra serpentina* (AMNH 107386), Chelydridae, no data. For other figures of this region see Kesteven, 1910, figures 23-25 (*Chelonia*); Ogushi, 1911, figures 19, 22, 23 (*Trionyx*). From Gaffney (1972b).

well-developed rostrum basisphenoidale with a comparatively long fused portion anterior to the sella turcica.

Living cheloniids are distinct from other turtles in having a rostrum basisphenoidale that is rodlike and raised off the floor of the basisphenium. In most other turtles the rostrum basisphenoidale lies on top of the median suture of the pterygoids to some extent, but in cheloniids most of the rostrum is raised above this suture. The embryology of the region in chelonioids is

quite different from other cryptodires and is of some systematic interest (see Development).

The lateral surface of the basisphenoid is a sutural face that usually contacts the pterygoid for most of its length. The prootic usually articulates along the posterolateral margin, and in living podocnemines the quadrate reaches the lateral face of the basisphenoid. In most turtles the passage of the canalis caroticus internus extends medially into the basisphenoid to reach the foramen anterius canalis carotici interni in

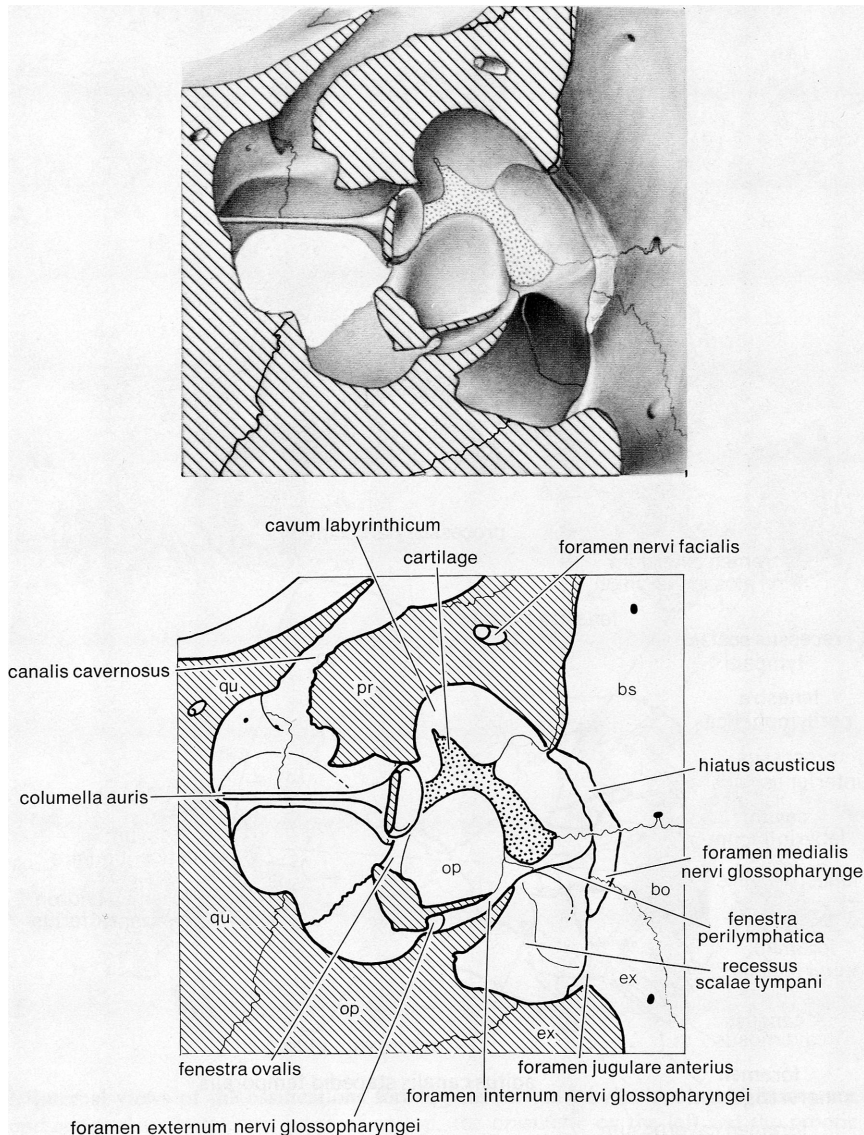


FIG. 50. Dorsal view of left otic region frontally sectioned in *Chelydra serpentina* (AMNH 67015), Chelydridae, Bronxville, Westchester County, New York. The foramen medialis nervi glossopharyngei is formed by the cartilage in the hiatus acusticus. This cartilage is gone in this specimen and the label indicates the position of the foramen. See also figures 64 and 87.

the sella turcica. In the podocnemine pleurodires the morphology of this area is considerably modified by the invasion of the canalis caroticus internus by a portion of the M.

pterygoideus (see Pterygoid). In baenoids the foramen posterior canalis carotici interni occurs about midway along the basisphenoid-pterygoid suture and the basisphenoid forms the medial

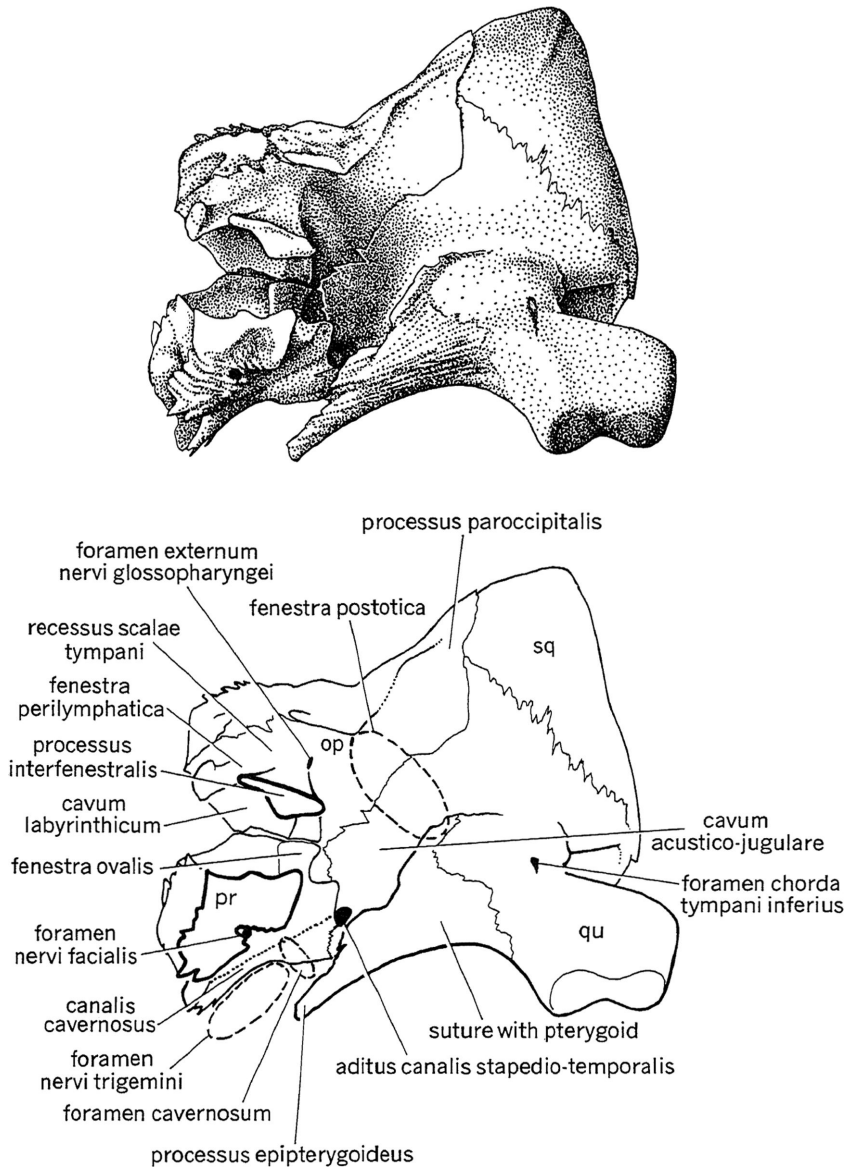


FIG. 51. Ventral view of right otic chamber, consisting of quadrate, squamosal, opisthotic, and prootic; with ventral elements removed to expose the cavum acustico-jugulare and cavum labyrinthicum. Posterior is toward top of page, lateral to the right. *Chelydra serpentina* (AMNH 107388), Chelydridae, no data.

portion of the foramen and nearly all of the canalis caroticus internus.

The ventral surface of the basisphenoid is

usually flat. In *Chelus*, however, it has a rounded ridge extending anteroposteriorly and cheloniids have more or less well-developed

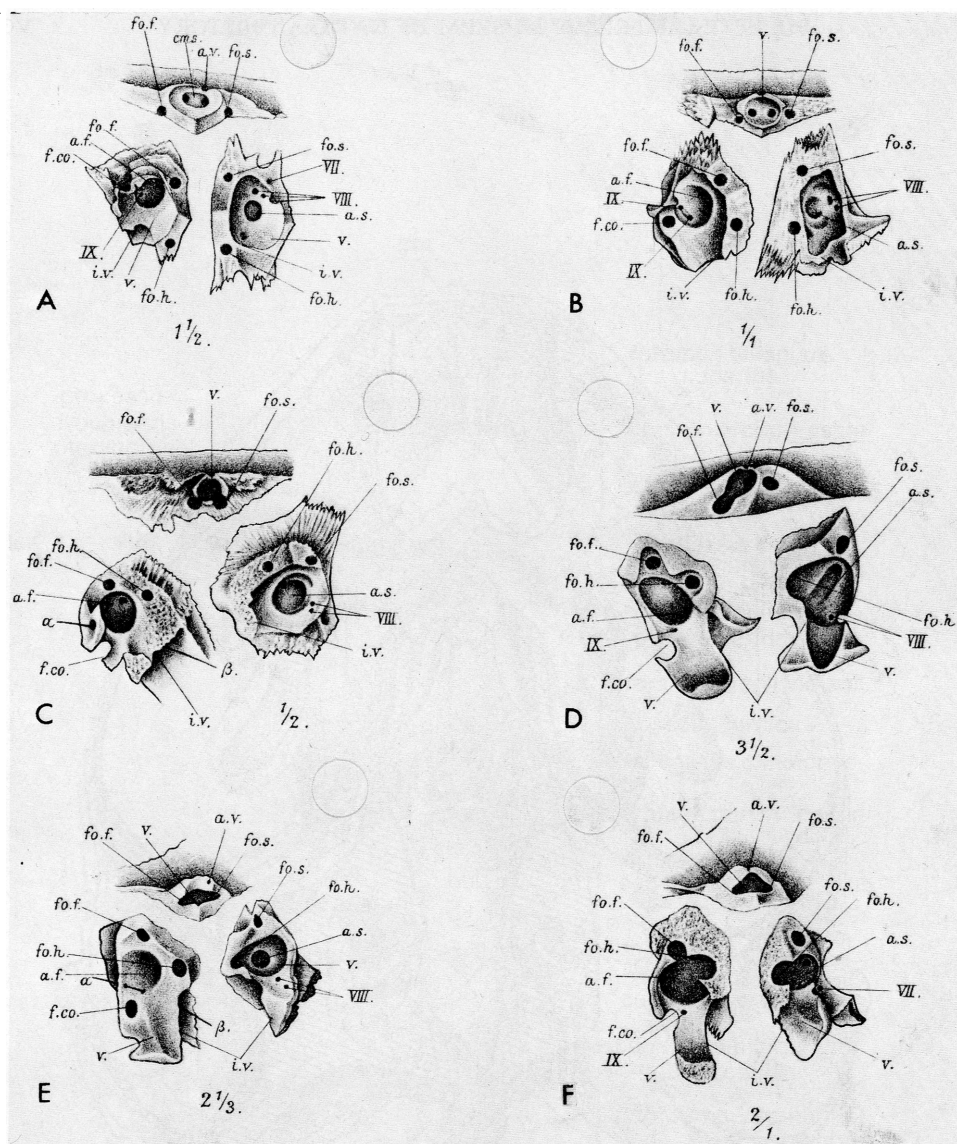


FIG. 52. Internal views of the ossifications forming the cavum labyrinthicum. All bones are of the left side with the supraoccipital (only the otic portion) on top, the opisthotic on the left and the prootic on the right in each figure. From Siebenrock (1897). A. *Chelodina longicollis*; B. *Trionyx sinensis*; C. *Macroclemys temminckii*; D. *Rhinoclemys* (*Nicoria* of Siebenrock) *punctularis*; E. *Emys orbicularis*; F. *Psammobates* (*Testudo* of Siebenrock) *oculifer*. Abbreviations: a.f., recessus labyrinthicus opisthoticus; a.s., recessus labyrinthicus prooticus; a.v., foramen aquaducti vestibuli; cms., commissure; f.co., fenestra perilymphatica; fo.f., canalis semicircularis posterior; fo.h., canalis semicircularis horizontalis; fo.s., canalis semicircularis anterior; v., recessus labyrinthicus supraoccipitalis; VII, foramen nervi facialis; VIII, foramen (or foramina) nervi acustici; IX, foramen internum nervi glossopharyngei; α—β, path of glossopharyngeal (IX) nerve.

grooves and ridges for muscle attachment sites (Kesteven, 1910, p. 384; for cervical muscle

information in *Lissemys* and *Geochelone elegans* see George and Shah, 1954, 1955).

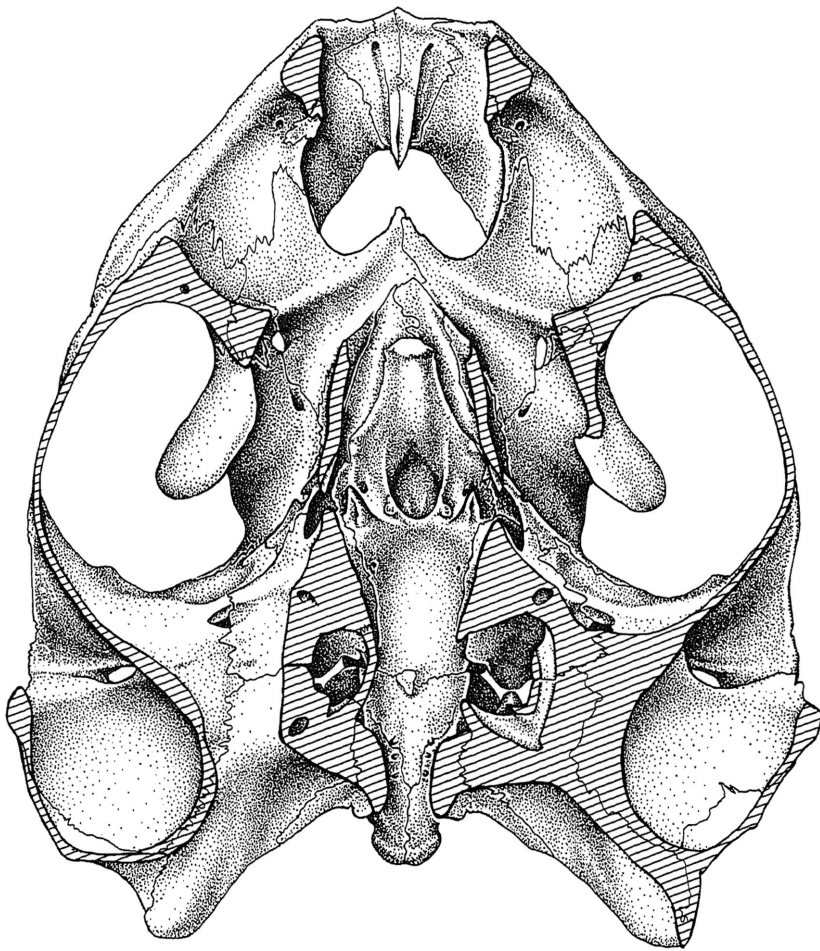
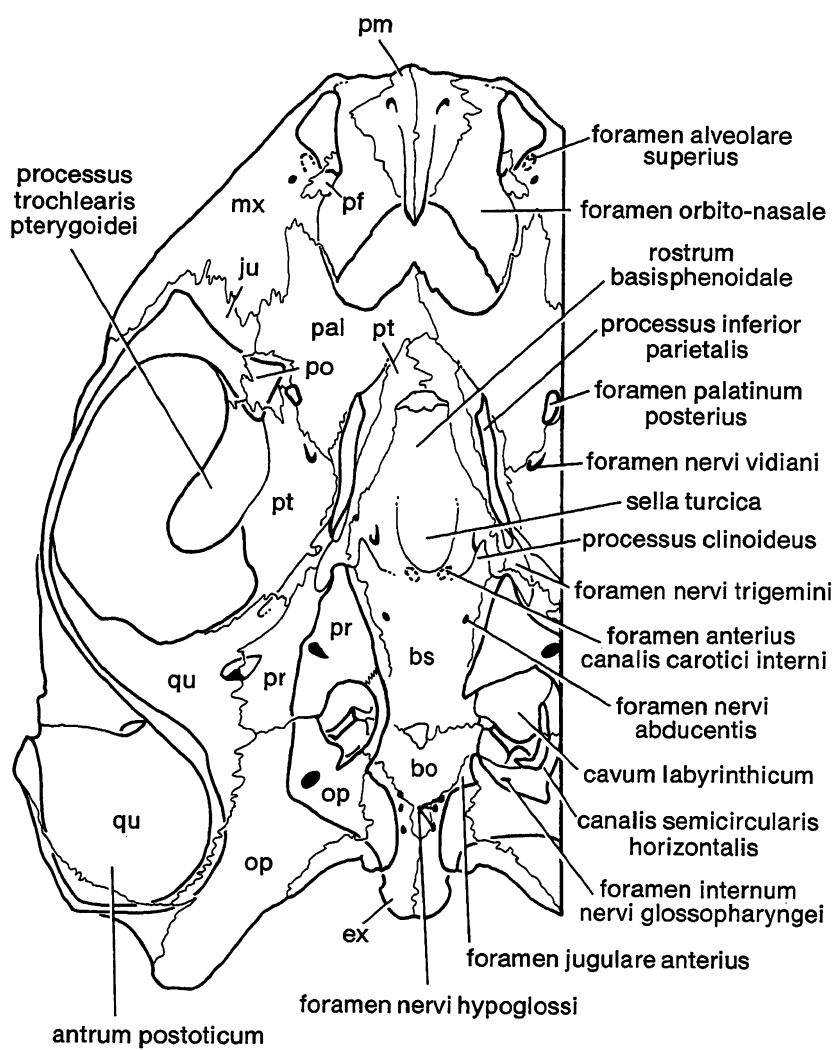


FIG. 53. *Pelusios* sp. (AMNH 10062, 55 mm.), Pelomedusidae, Faradje, Haut-Zaire, Zaire. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces.



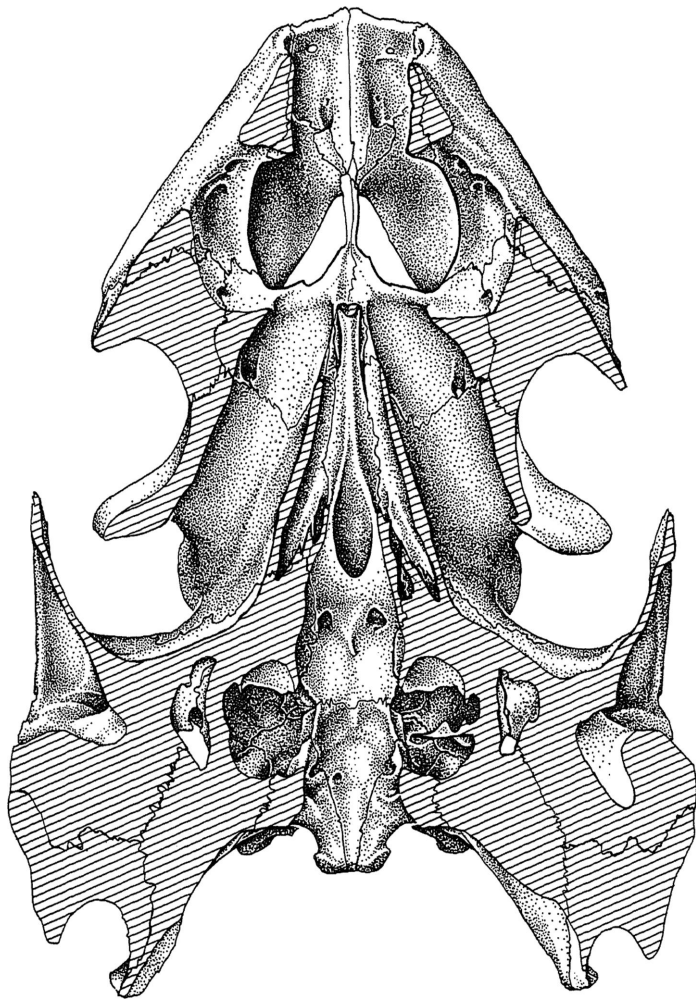
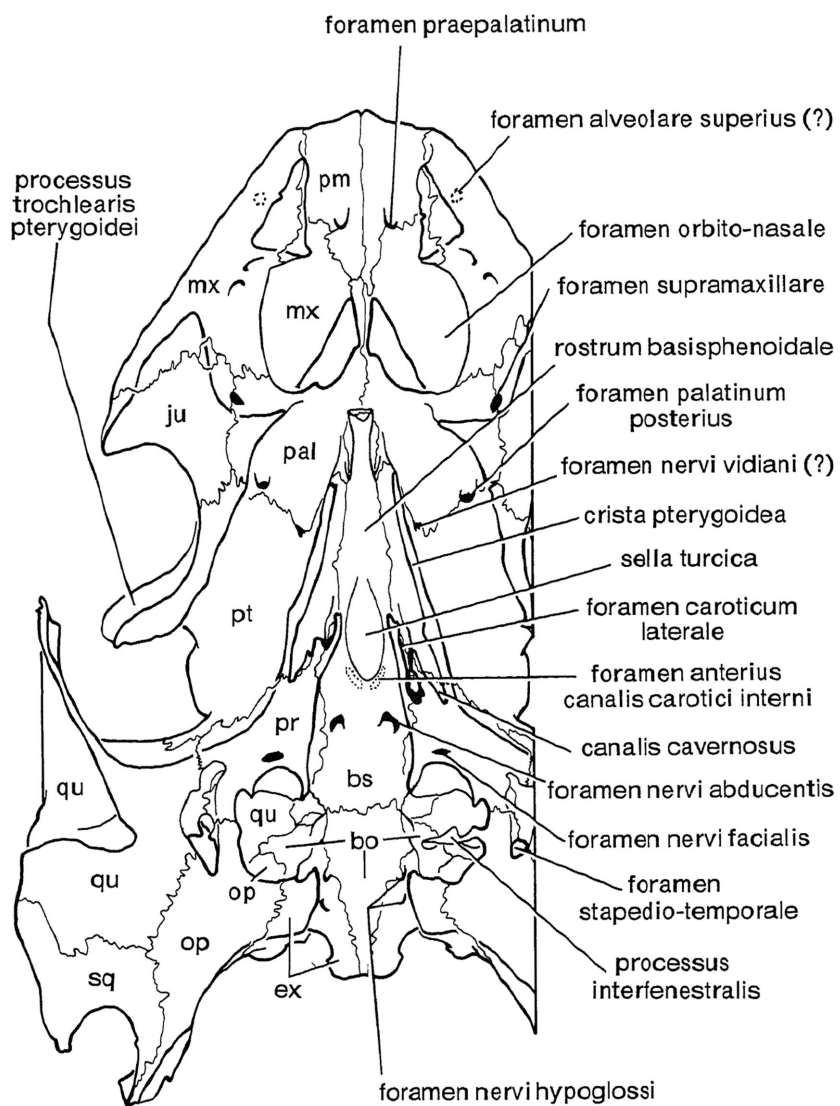


FIG. 54. *Podocnemis expansa* (AMNH 97124, 126 mm.), Pelomedusidae, Rio Mamoré, Beni, Bolivia. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. Elongate opening identified as the foramen caroticum laterale is continuous with the hypertrophied pterygoideus muscle chamber characteristic of *Podocnemis* and its near relatives (see Pterygoid.)



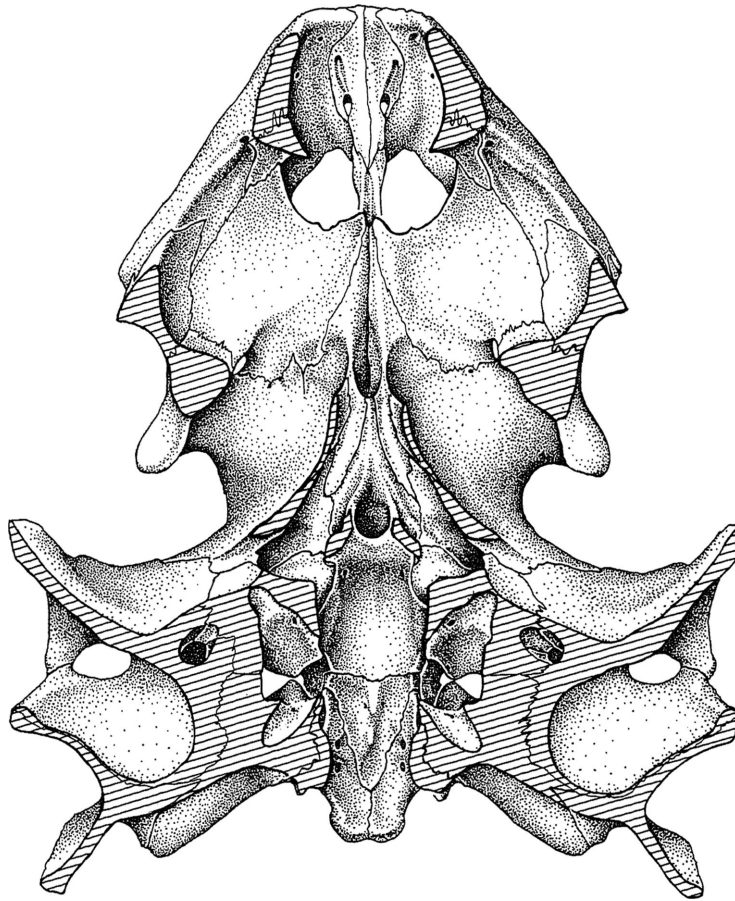
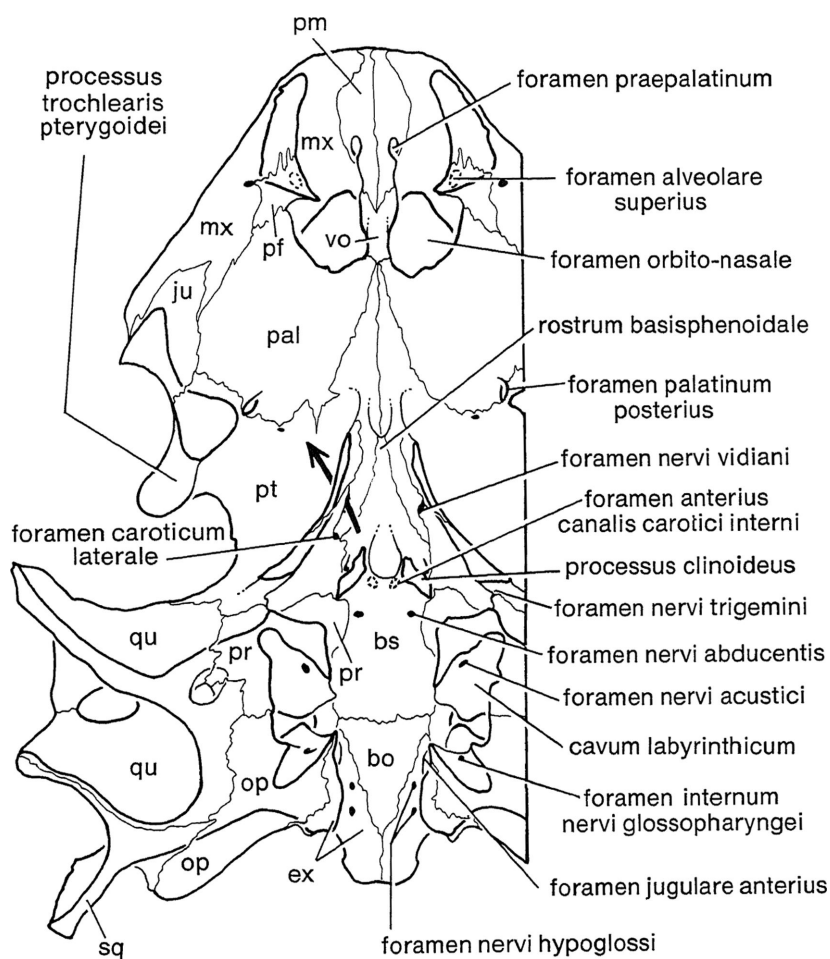


FIG. 55. *Elseya latisternum* (AMNH 103700, 53 mm.), Chelidae, Brisbane, Queensland, Australia. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. Arrow shows position of canal penetrating crista pterygoidea and questionably identified as the canalis nervi vidiani.



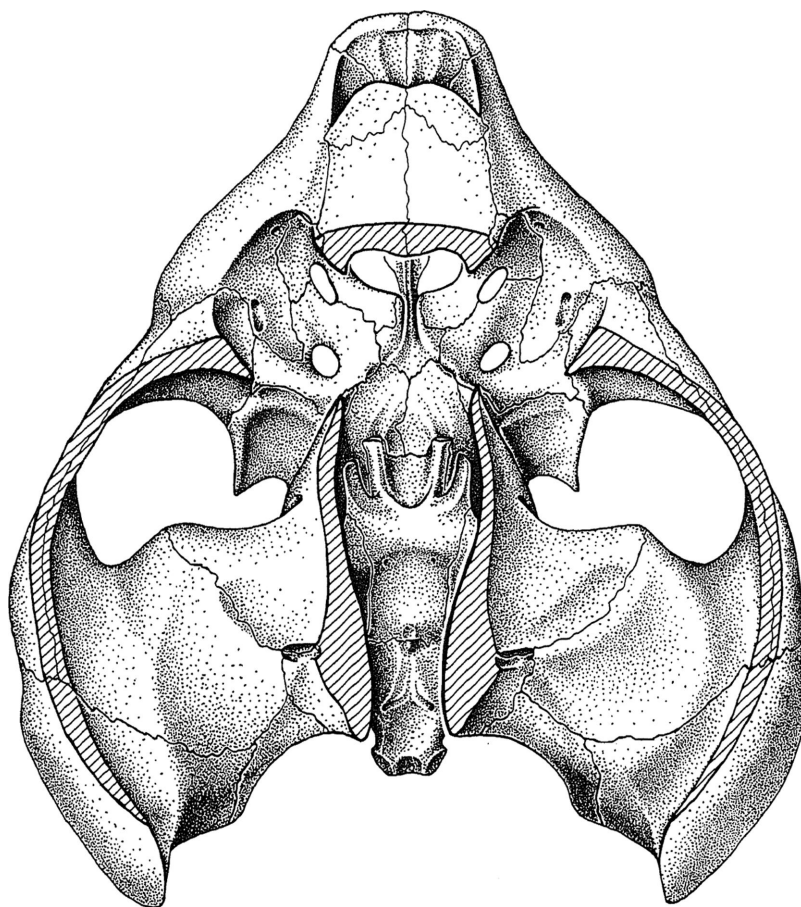
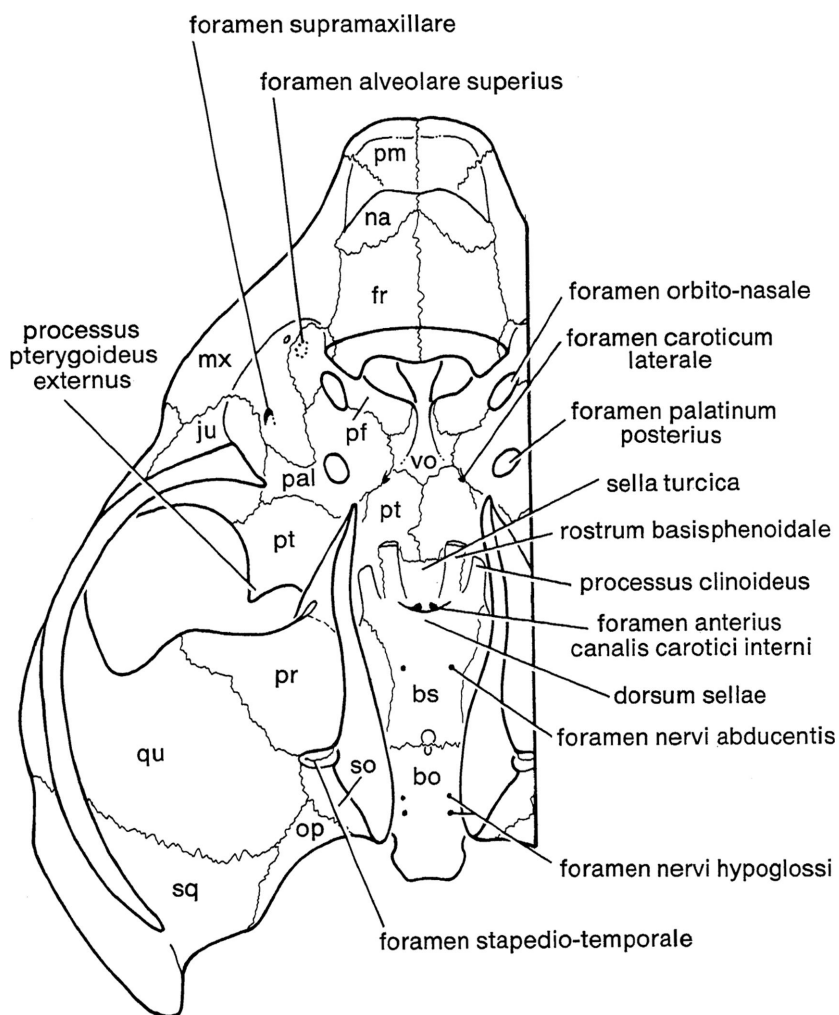


FIG. 56. *Eubaena cephalica* (composite based on AMNH 4948, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana; and YPM 1785, Lance Formation, Niobrara County, Wyoming), Baenidae, Late Cretaceous. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. Condyle-premaxilla length of YPM 1785 is 66 mm.



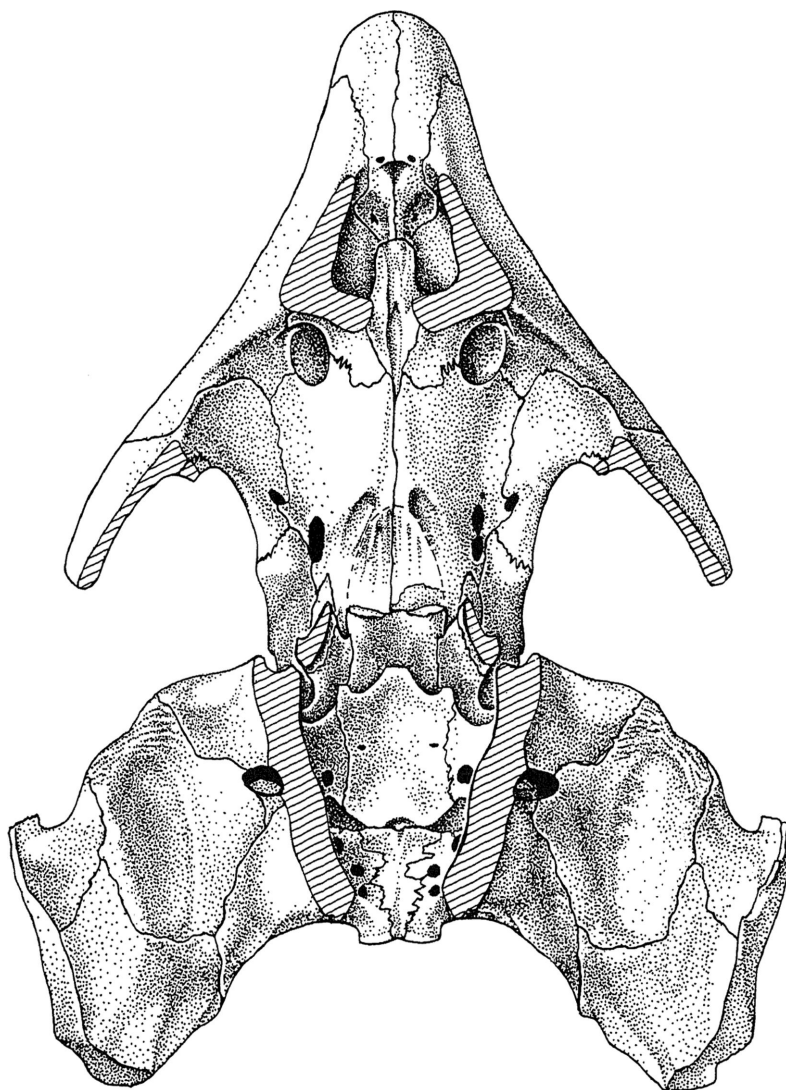
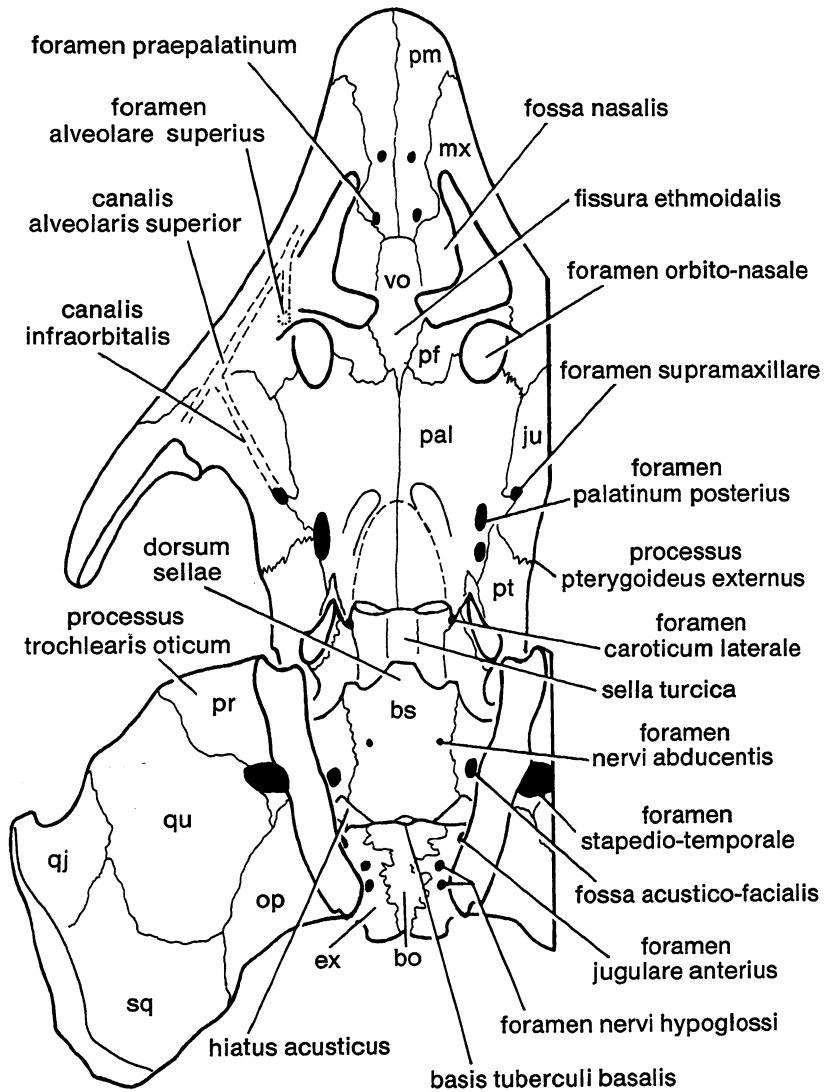


FIG. 57. *Solnhofia parsonsi* (Teyler Museum 4023, 73 mm.), Solnhofen Formation,? Late Jurassic, Germany? Eucryptodire, family indet. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. From Gaffney (1975c).



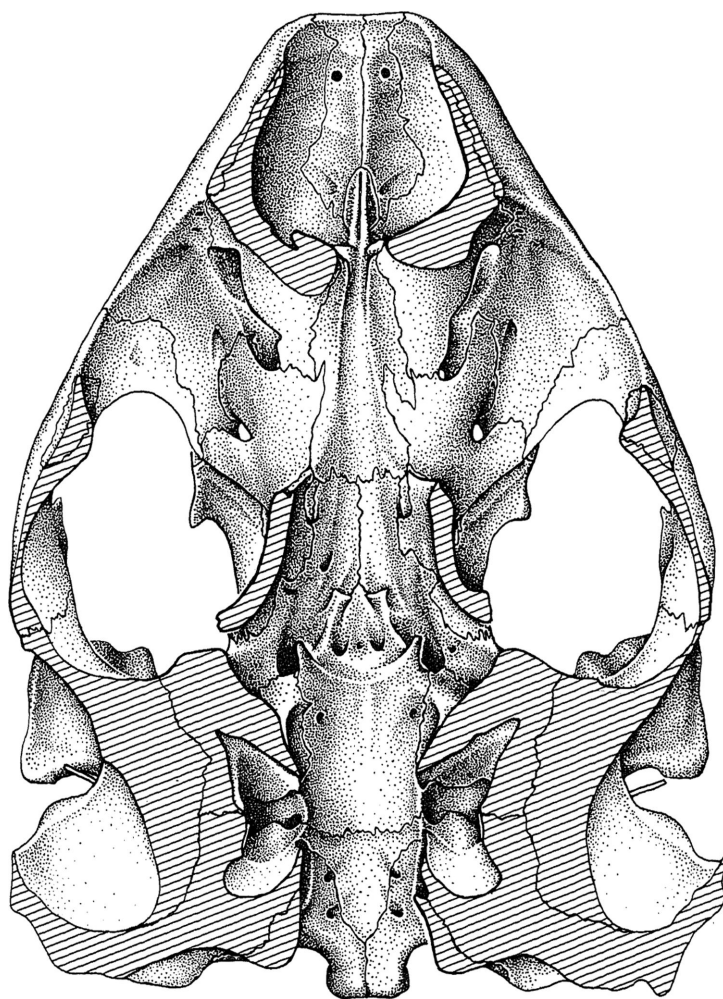
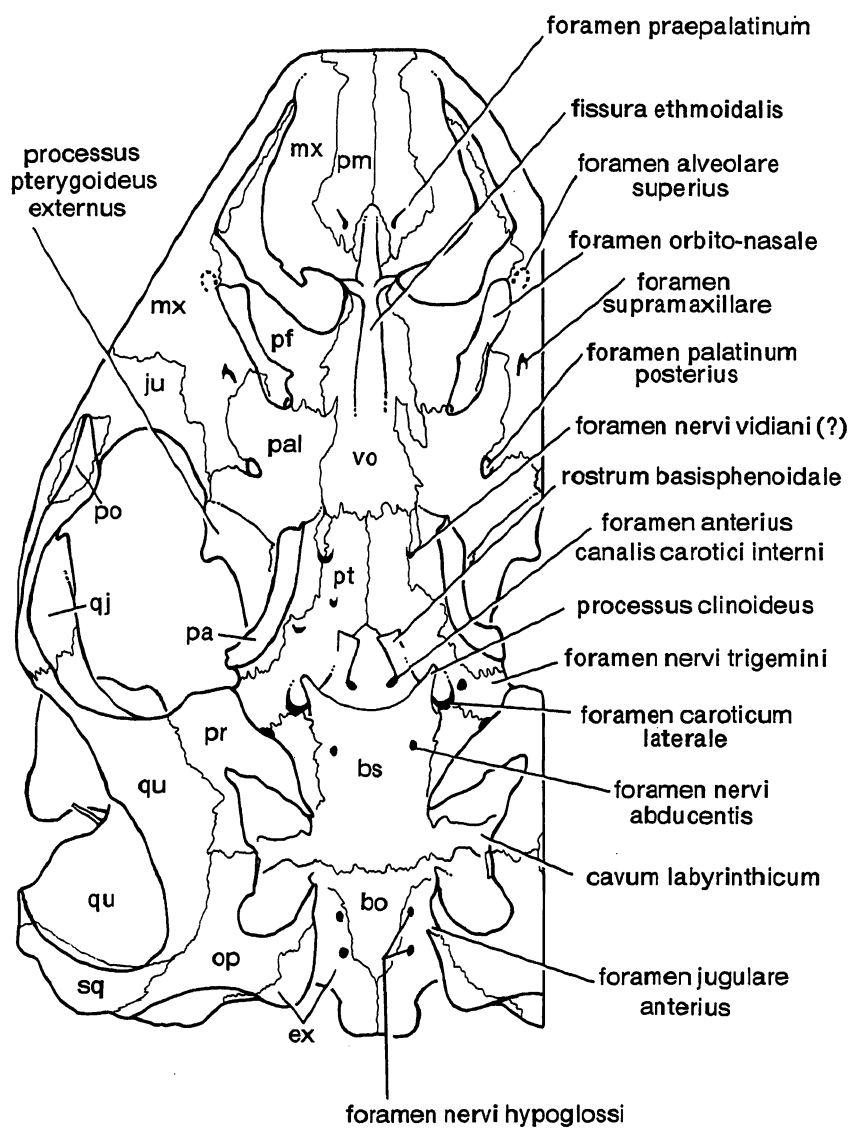


FIG. 58. *Dermatemys mawii* (NMNH 66666, 71 mm.), Dermatemydidae, "Tehuantepec," Mexico. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. The structure labeled foramen nervi vidiani has not been identified on the basis of dissection and should be considered questionable. The three foramina (unlabeled) in the floor of the left sulcus cavernosus are also questionable in content, they appear to be continuous with each other and with foramina on the ventral surface of the pterygoid.



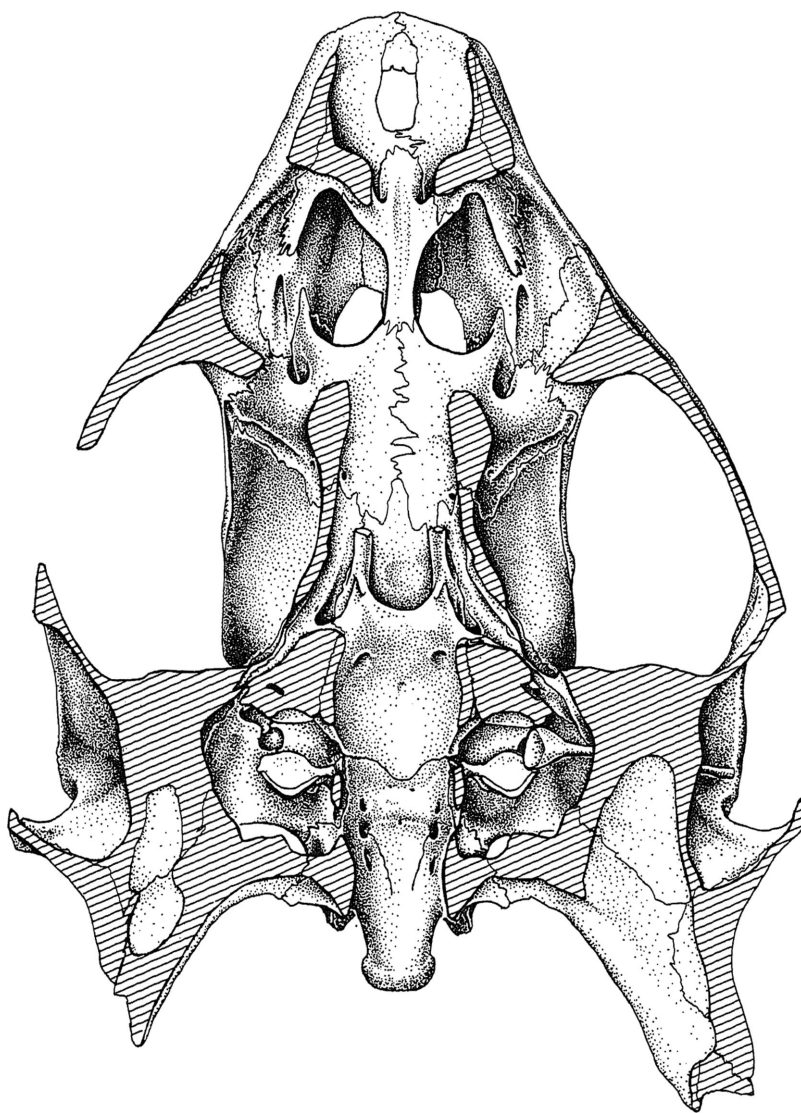
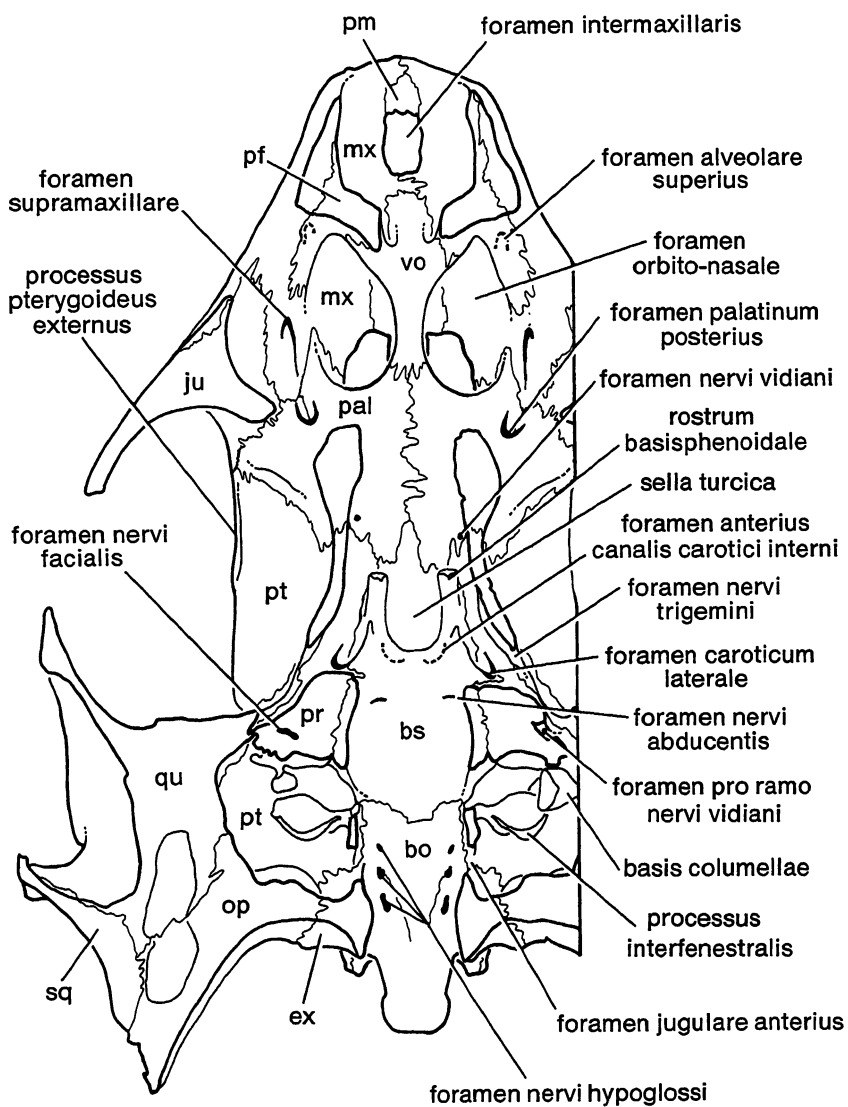


FIG. 59. *Trionyx cartilagineus* (AMNH 28357, 112 mm.), Trionychidae, 53 mi. E of Um Pang, Thailand. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. Right columella auris is present, left is absent.



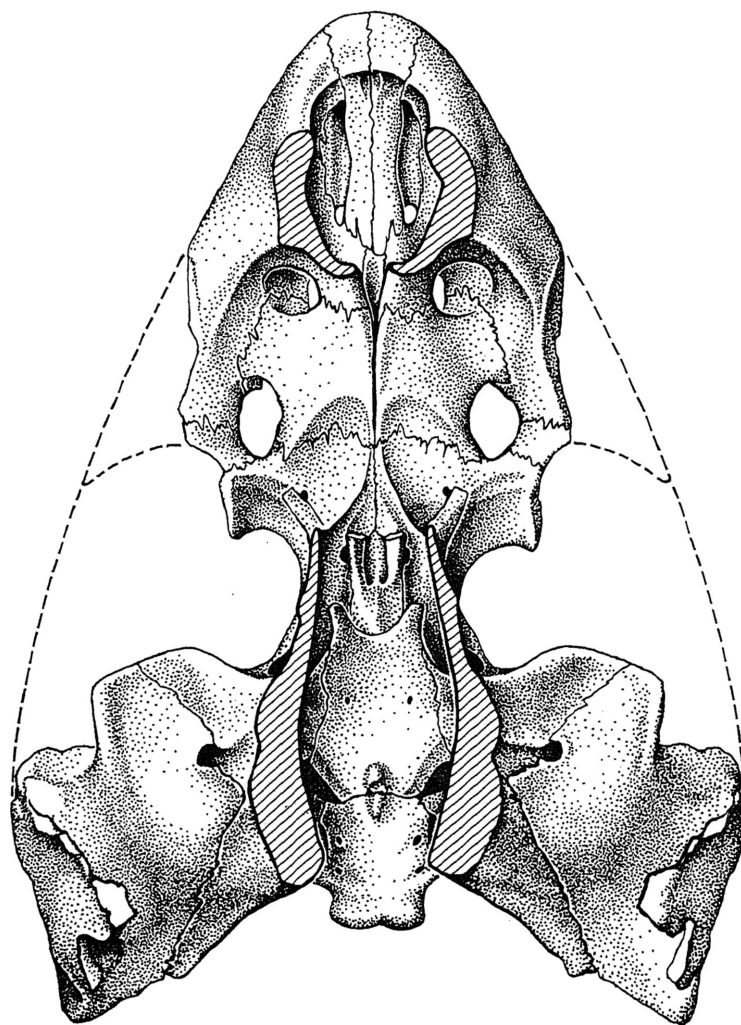
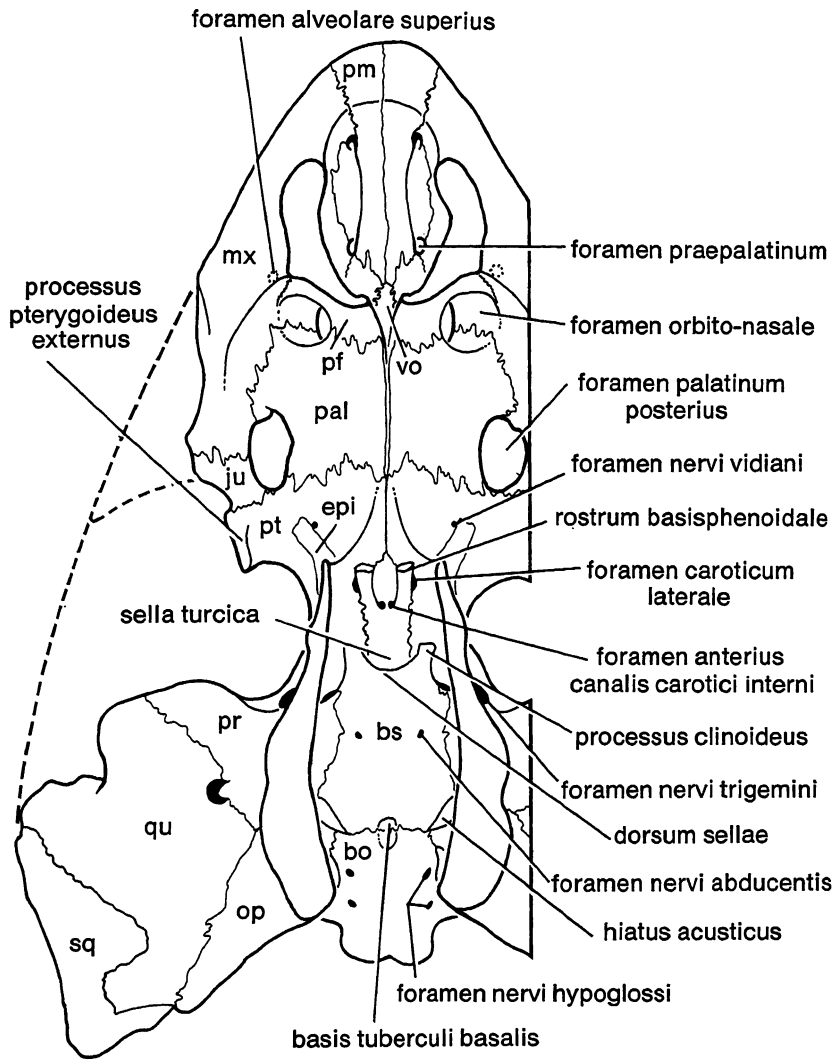


FIG. 60. *Portlandemys mcdowelli* (based on BMNH R2914 and R3164), Plesiochelyidae, Portland Formation, Late Jurassic, Great Britain. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surface. From Gaffney, 1976.



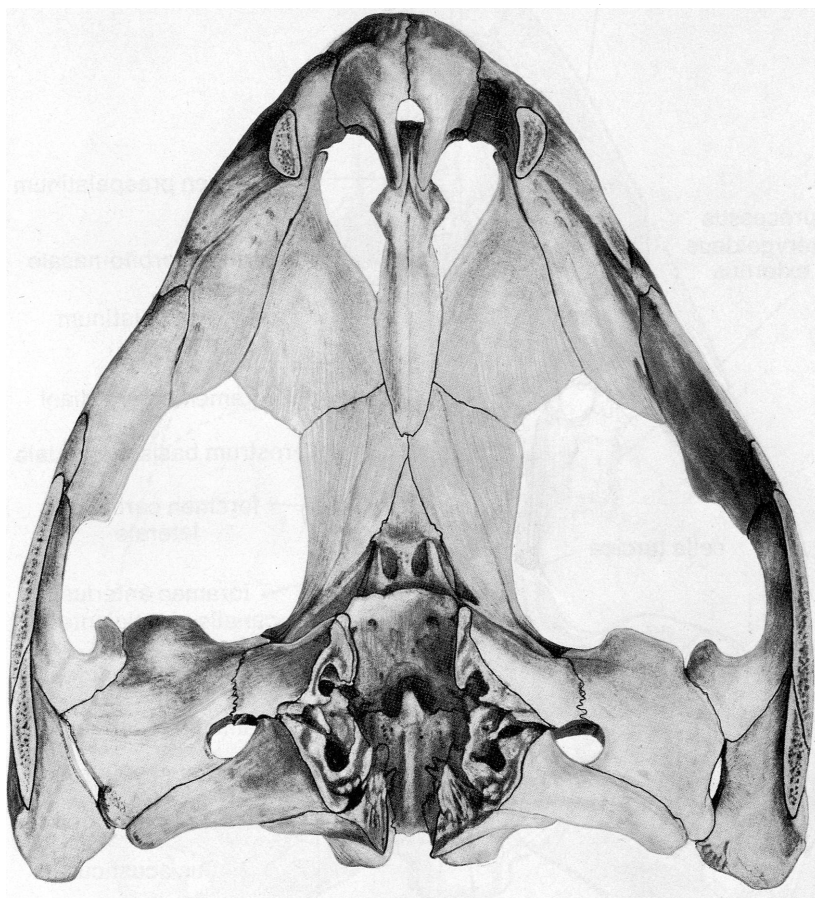
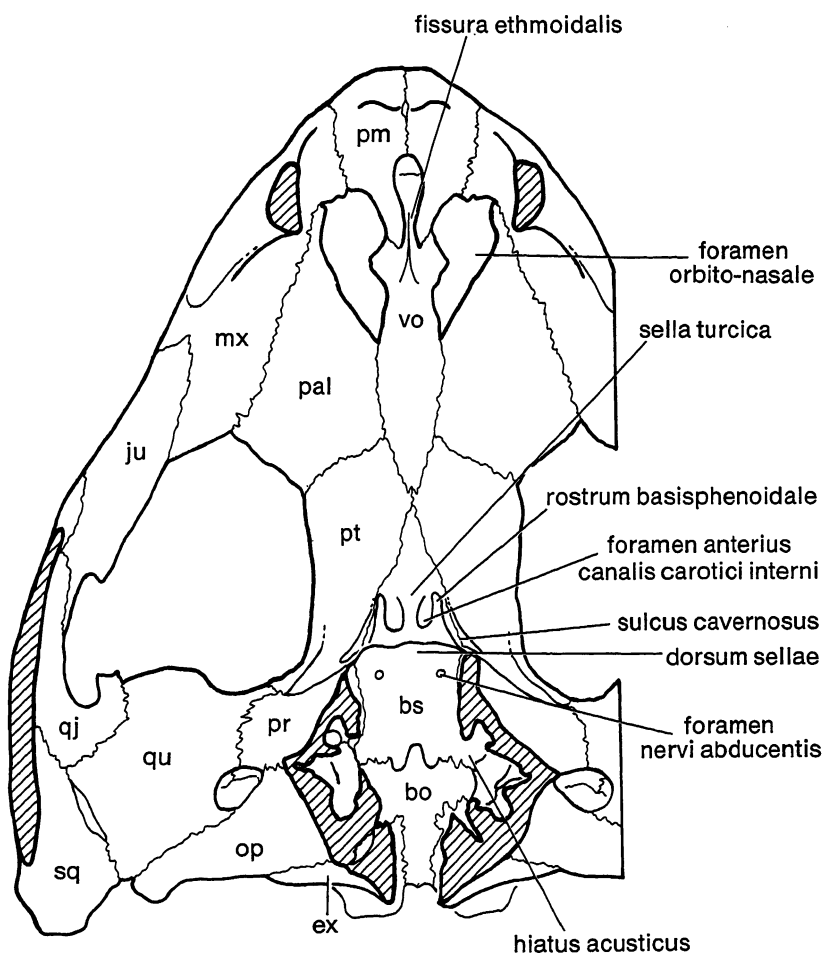


FIG. 61. *Dermochelys coriacea*, Dermochelyidae, Portuguese coast, Atlantic Ocean. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surface. From Wegner (1959, pl. 6).



icranial foramina, ear structures, and lower jaw (nearly all are repeated in this paper). Albrecht (1976) described the cranial arteries and foramina in *Chelydra*. Gaffney (1975d) also has a series of sections (for comparison with a similar series of sections in a pleurodire, neither series is reproduced here) and good halftones of the neurocranial ossifications in *Chelydra*. Overall skull views are available in Gray (1855), Boulenger (1889), and Gaffney (1975e). My inclusion of *Platysternon* in the Chelydridae is suggested in Gaffney (1975e) and this paper follows the classification in that paper (*q.v.* for earlier references). Rieppel (1976, 1977) presented developmental infor-

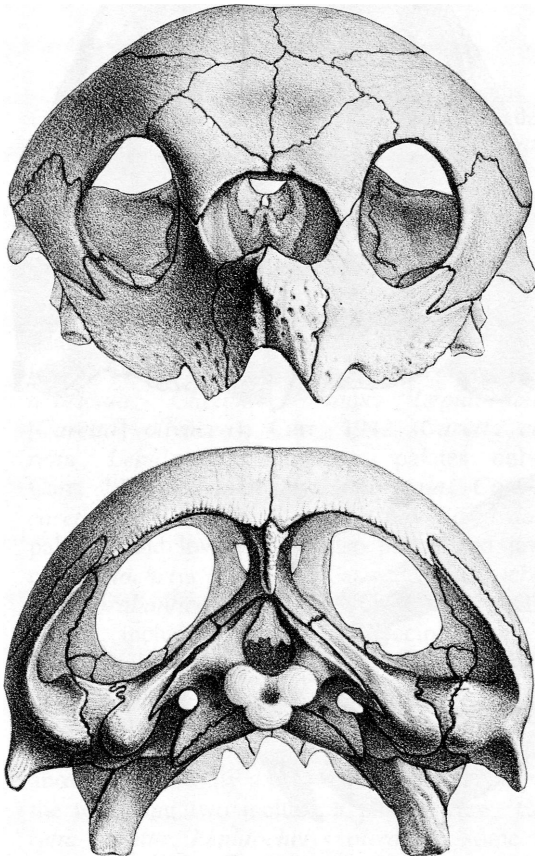


FIG. 202. *Dermochelys coriacea*, Dermochelyidae. Modified from Gervais (1872).

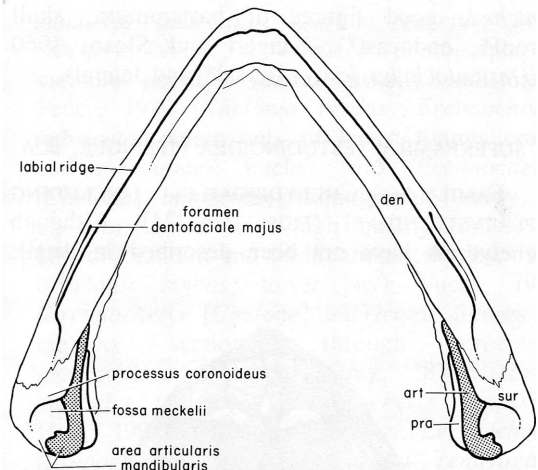


FIG. 203. *Dermochelys coriacea* (AMNH 57749), Dermochelyidae, no data. Dorsal view of lower jaw, cartilage stippled. Restored from Wegner (1959). Unossified articular is characteristic of *Dermochelys*.

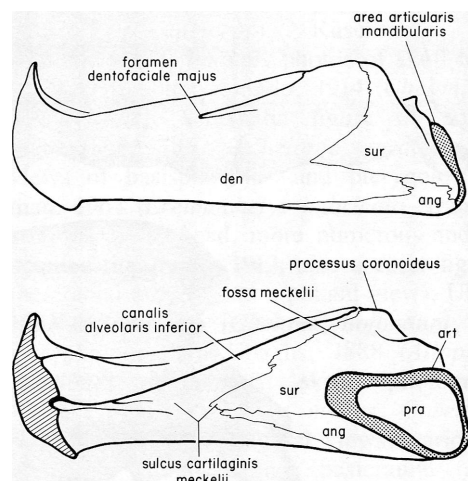
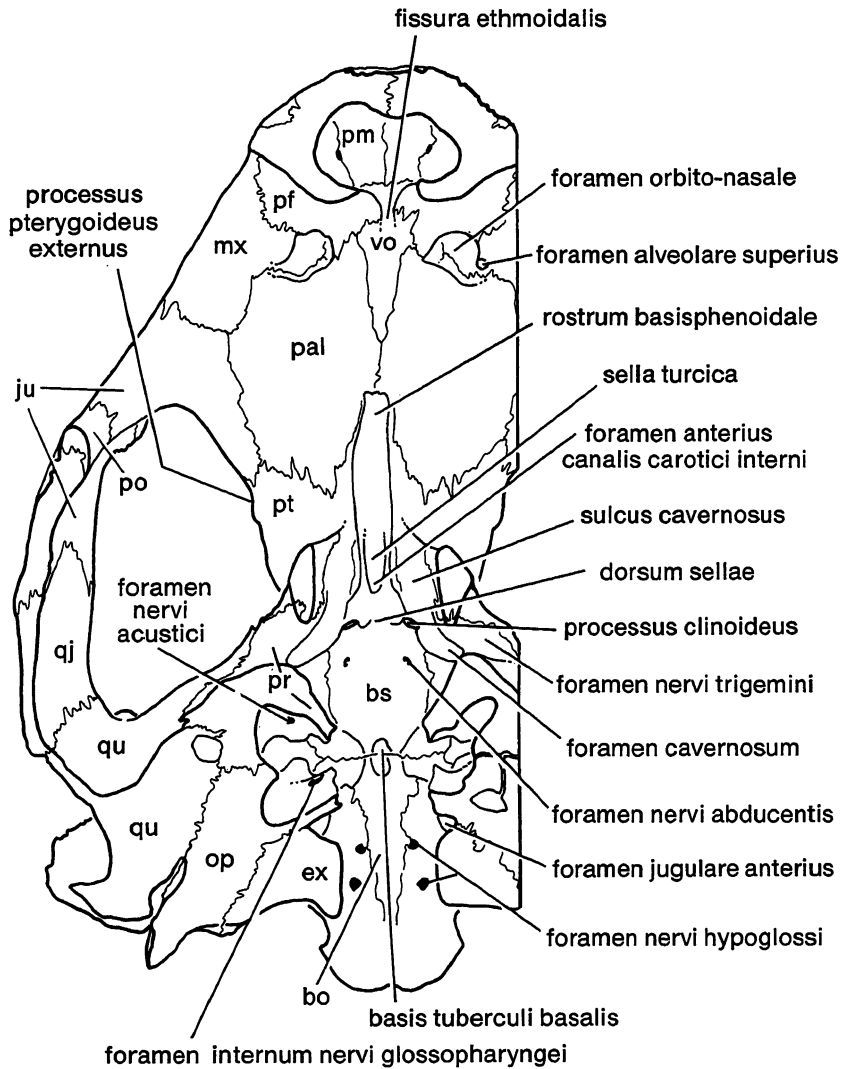


FIG. 204. *Dermochelys coriacea* (AMNH 57749), Dermochelyidae, no data. Upper, lateral view of left lower jaw ramus; lower, medial view of right lower jaw ramus. Cartilage stippled. Restored from Wegner (1959). See also Poglayen-Neuwall (1953) for medial view of jaw with cartilage and nerves indicated.



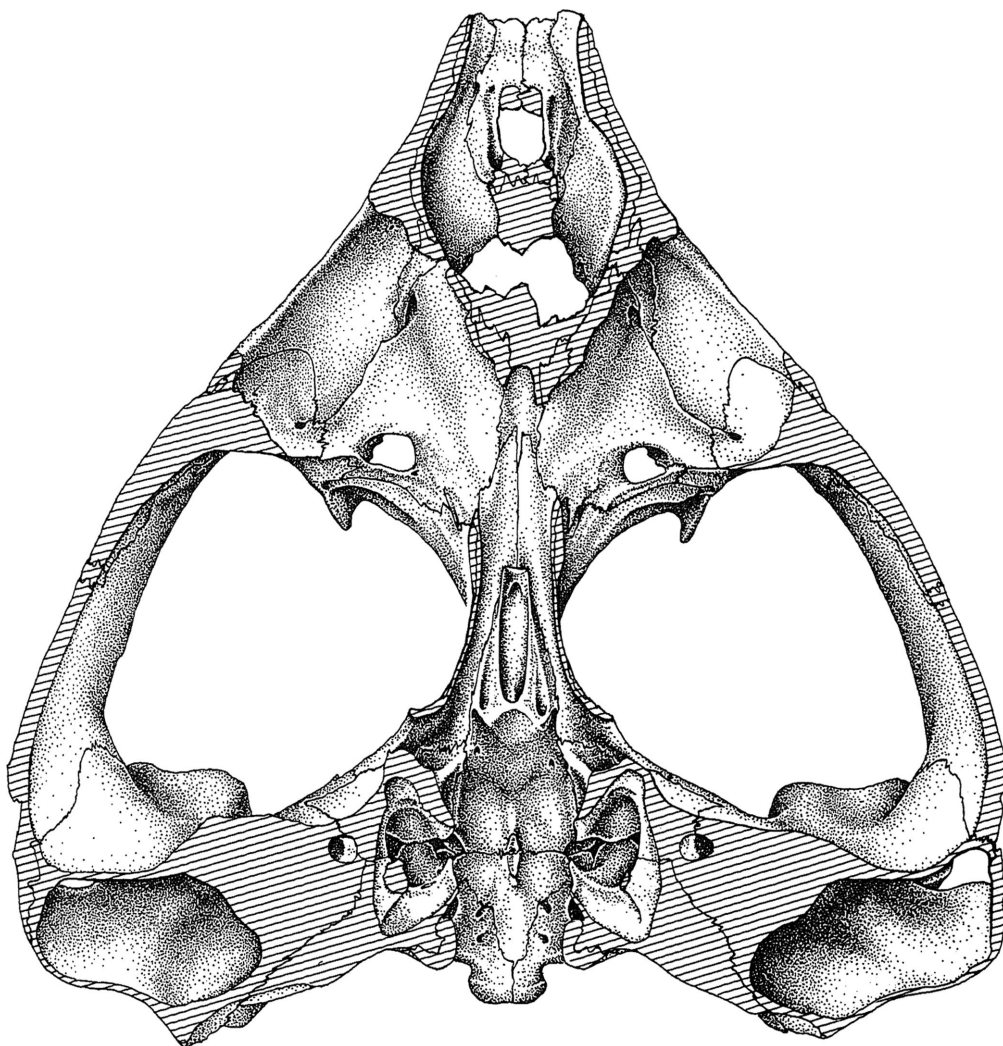
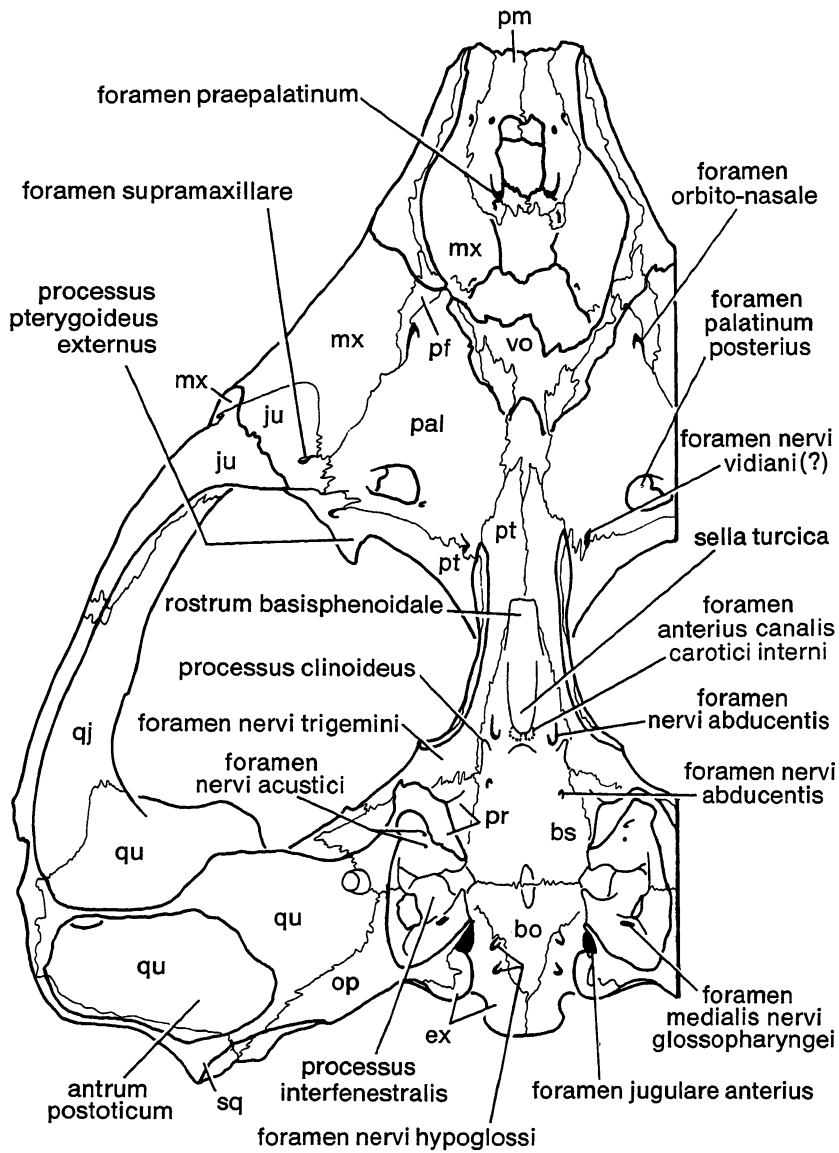


FIG. 63. *Platysternon megacephalum* (AMNH 30123, 58 mm.), Chelydridae (Gaffney, 1975e), Nodda, Hainan Island, Kwangtung Province, Peoples' Republic of China. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surface.



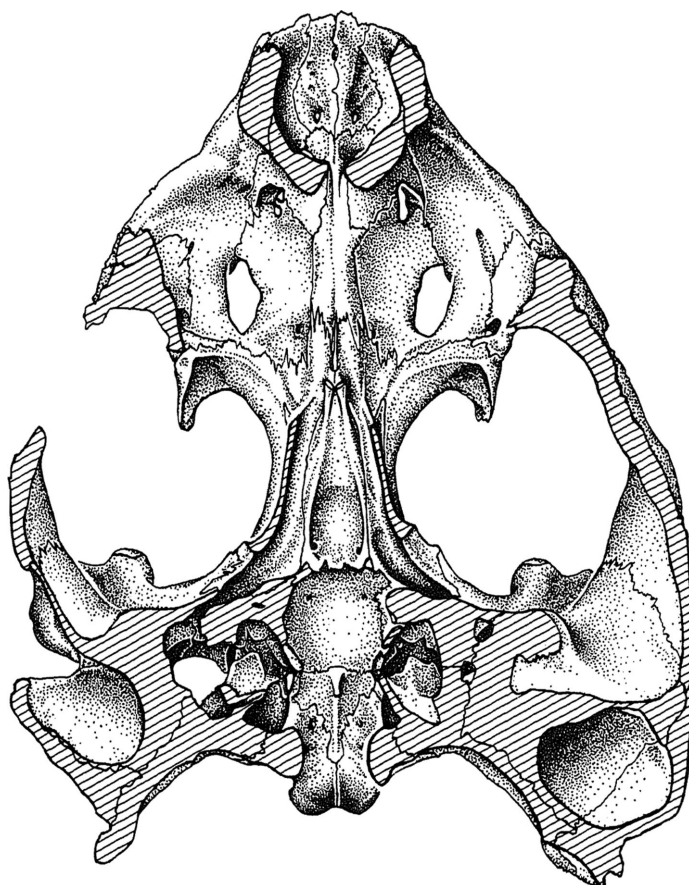
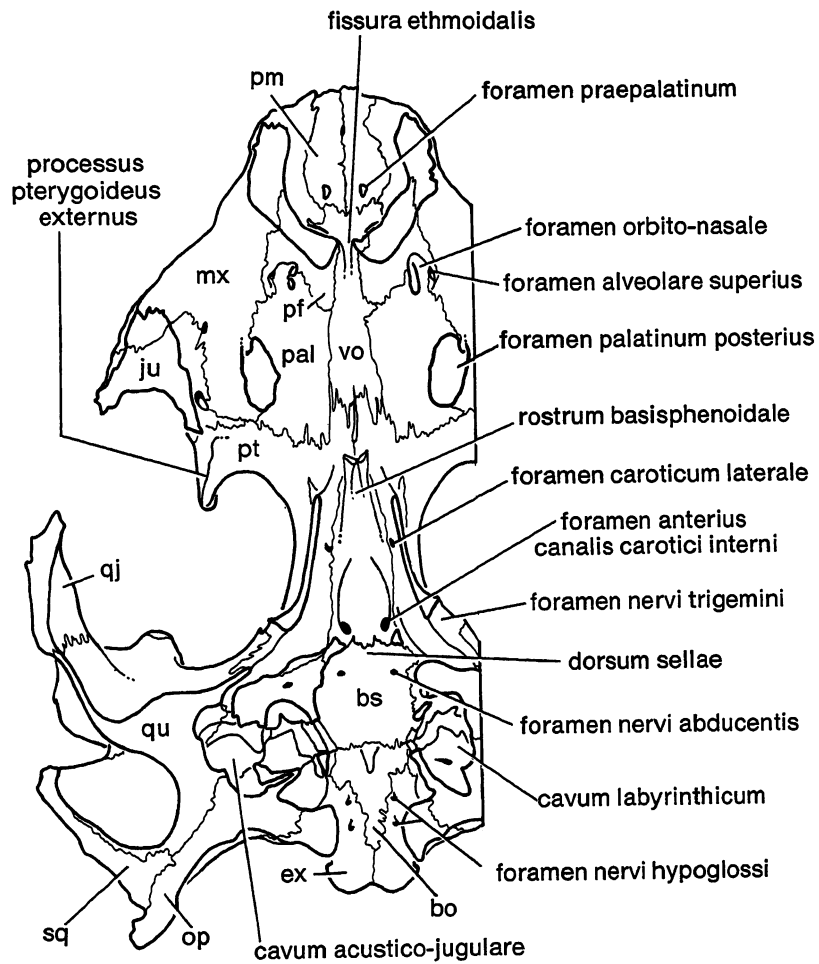


FIG. 64. *Chelydra serpentina* (AMNH 67015, 101 mm.), Chelydridae, Bronxville, Westchester County, New York. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surfaces. The skull is asymmetrical anteriorly due to a pathologic condition of the left orbit.



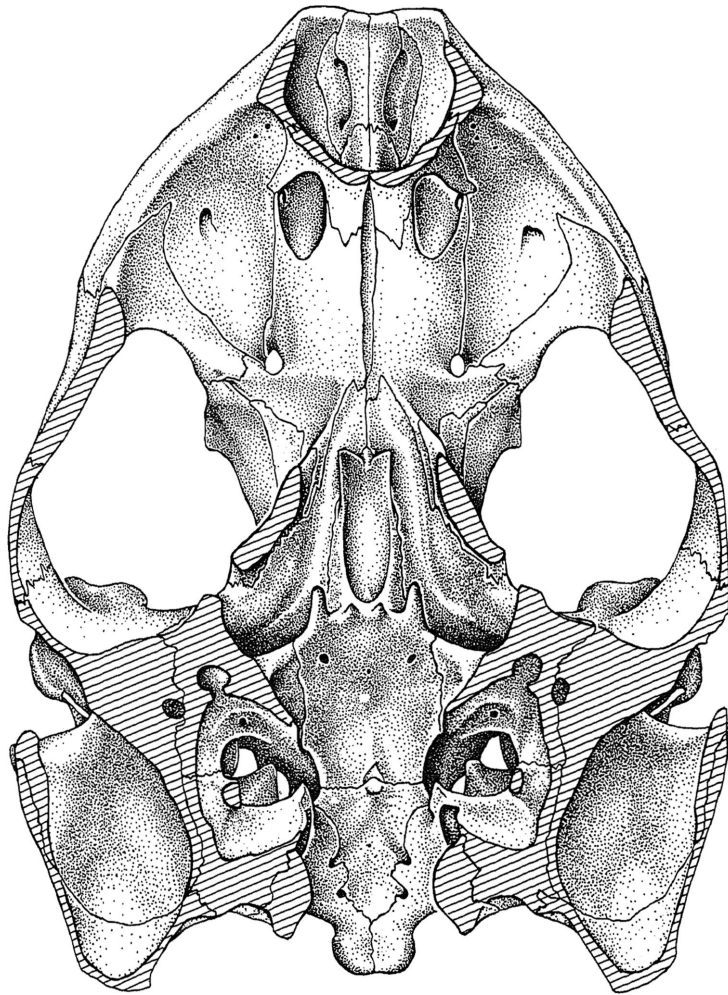
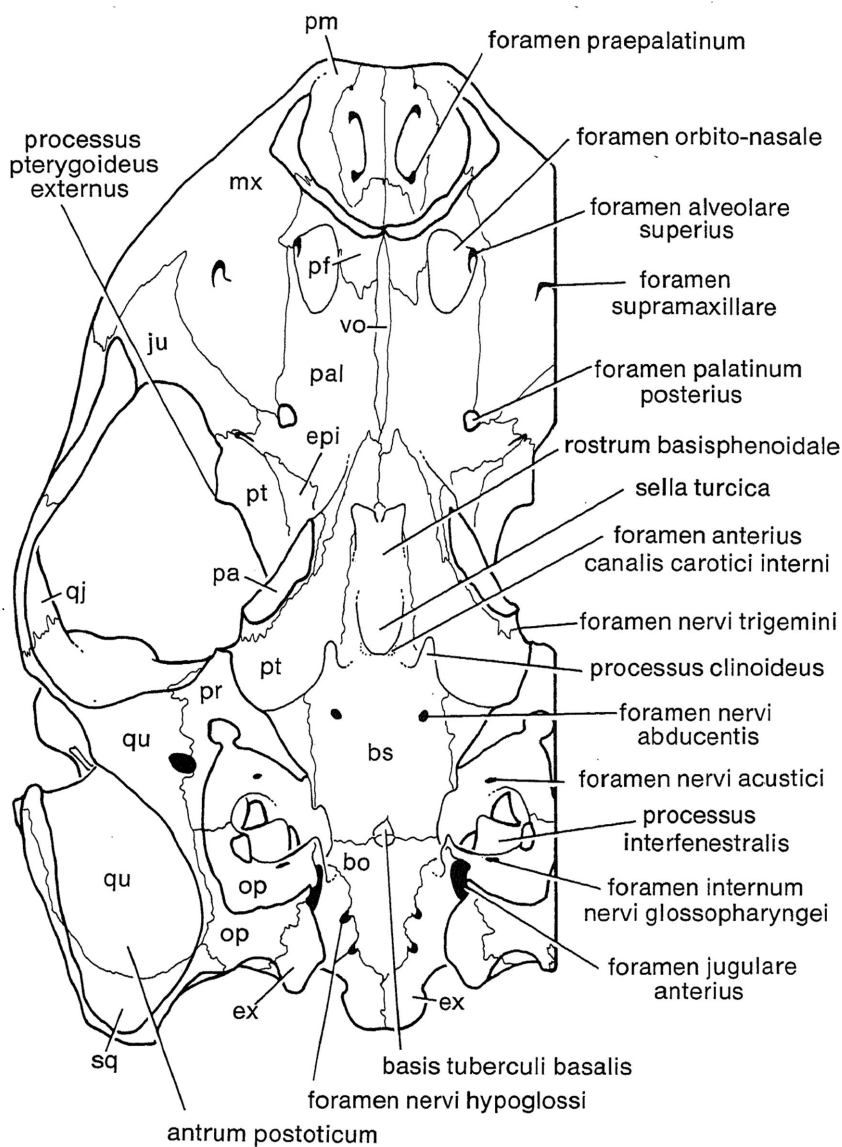


FIG. 65. *Chrysemys concinna* (AMNH 111960, 44 mm.), Emydidae, Colorado River, Travis County, Texas. Dorsal view of horizontally sectioned skull. Hatched areas indicate cut surface.



CAVUM LABYRINTHICUM

Figures 45, 49-65, 105-109

The bones forming the inner ear capsule in turtles are fairly consistent in morphology. The variation that does occur, however, would appear to be due primarily to the extent of ossification developed in the adult. Although taxonomically diverse studies of chelonian inner ear soft structures are lacking, the work to date supports the contention that the inner ear soft structures of living turtles are quite similar to one another and few differences have been noted. However, the bones containing the inner ear soft structures differ in the degree to which bone has replaced the chondrocranial otic chamber. The chondrocranium itself is probably quite consistent in all turtles in the inner ear region.

The cavum labyrinthicum (figs. 105/109) may be separated into two major regions: a dorsal vestibular area housing the semicircular canals and a ventral cochlear area containing the sacculus, lagena and other endolymphatic and perilymphatic structures (fig. 50). The dorsal vestibular region is the more complicated osteologically, as it contains the variably ossified cartilage surrounding the semicircular canals. Anteriorly the prootic, posteriorly the opisthotic, and dorsally the supraoccipital, form the vestibular region in the bony skull (fig. 52). The canalis semicircularis anterior extends from the recessus labyrinthicus supraoccipitalis to the recessus labyrinthicus prooticus and is formed by the supraoccipital and prootic. Similarly, the canalis semicircularis horizontalis extends from the recessus labyrinthicus prooticus to the recessus labyrinthicus opisthoticus and is formed by the prootic and opisthotic, whereas the canalis semicircularis posterior extends from the recessus labyrinthicus supraoccipitalis to the recessus labyrinthicus opisthoticus and is formed by the supraoccipital and opisthotic. Each recessus mentioned above is a concavity in the bone indicated that contains the following: recessus labyrinthicus opisthoticus—the posterior semicircular canal ampulla and union of the posterior and horizontal semicircular canals; recessus labyrinthicus prooticus—the anterior and horizontal semicircular canal ampullae; recessus

labyrinthicus supraoccipitalis—the union of the anterior and posterior semicircular canals. The canals and ampullae are variably enclosed by bone. Siebenrock (1897, p. 271, pl. III) has described and figured examples of this variation. He considered *Chelodina* to have the most ossified inner ear and "*Testudo*" (*sensu lato*) to have the least ossified. In most pleurodires the semicircular canals are completely formed in bone, whereas in many cryptodires the ossification around the canals is reduced resulting in a sulcus or groove instead of a canal.

The dorsal vestibular portion of the chelonian inner ear is basically quite similar to other reptiles, however, the more ventral cochlear portion contains important differences between turtles and other vertebrates. This ventral portion contains the sacculus, lagena, and elements of the perilymphatic system. The bony record of these structures is usually wanting. Even in a cartilaginous preparation of a fully adult *Che-lydra* it is not possible to accurately delimit these soft structures within the ventral portion of the inner ear (the position of entry and exit of structures can be determined, however).

The limits of the ventral portion of the inner ear usually have more cartilaginous material than the vestibular portion. The dorsal portion is always enclosed by bone, but the ventral part may appear open to the outside if the cartilage is removed. Most living pleurodires (except *Podocnemis* and its near relatives) have the cavum labyrinthicum open ventrally between the opisthotic and prootic. This part of the floor may be completed in many cryptodires by the meeting of the opisthotic and prootic, with variable contributions from the basisphenoid. With the cartilage removed the cavum labyrinthicum of many cryptodires is floored by parts of the pterygoid and basioccipital also. The pterygoid may, at least in trionychids, form a distinct true floor of the cavum labyrinthicum, whereas the basioccipital usually has a very limited exposure in the postero-ventromedial area just below the hiatus acusticus.

Bramble (1971) has reported hypertrophy of the middle ear and a saccular otolith in *Gopherus polyphemus* and *G. flavomarginatus*.

This hypertrophy has resulted in other changes in the otic region including ventral exposure of the processus interfenestralis.

ACOUSTIC NERVE FORAMINA

The openings into the cavum labyrinthicum are for nerves and auditory structures. The acoustic (VIII) nerve penetrates the medial wall of the cavum and innervates the inner ear structures. DeBurlet (1934, fig. 1190) indicated the way in which the inner ear structures are innervated and shows three branches of the acoustic (VIII) nerve entering the inner ear. Siebenrock (1897, p. 270) says that *Cyclernys* and "*Testudo*" (*sensu lato*) have only one branch entering the cavum. However, a specimen of *Geochelone elephantopus* (AMNH 75043) has two foramina in the prootic for the acoustic nerve, and more may have been cartilaginous. Soliman (1964, pp. 256-257) also describes three branches in *Eretmochelys* and *Chelydra*. A specimen of *Trionyx* (AMNH 28357) has one large and four minute (only three on the other side) ossified foramina apparently containing branches of the acoustic nerve or nutrient ves-

sels. Ogushi (1911, figs. 16, 23) indicates four foramina in bone. The cartilaginous foramina that may be present in the hiatus acusticus are indicated by Soliman (1964, fig. 1—*Chelydra serpentina*; fig. 2—*Eretmochelys imbricata*) and by Nick (1912, fig. 17—*Dermochelys coriacea*; fig. 19—*Chelonia mydas*; fig. 21—*Chelydra serpentina*). Although Soliman's *Eretmochelys* figure is apparently new, his figure of *Chelydra* seems to be largely taken from Nick with, however, an important difference. Nick labels one cartilaginous foramen in the hiatus acusticus as containing both the glosopharyngeal (IX) nerve and a branch of the acoustic (VIII) nerve. This is probably a mistake and is corrected by Soliman who indicates that the acoustic (VIII) nerve penetrates the otic chamber in three places, one of which may be partially formed in cartilage and lies at the anterior edge of the hiatus acusticus. In summary, it appears that at least two and usually three branches of the acoustic nerve enter the cavum labyrinthicum and that part of these may lie in the cartilaginous hiatus acusticus and be absent in the bony skull. The relative position

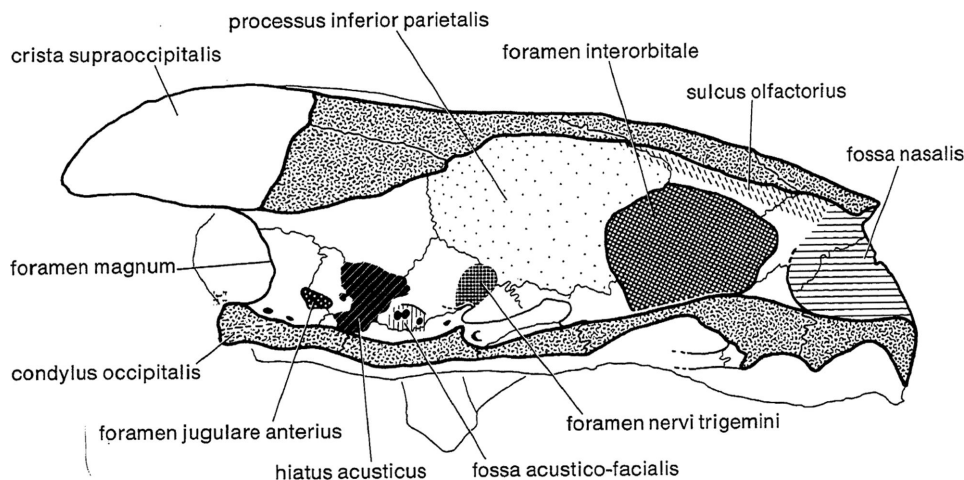


FIG. 66. Prominent structures visible in a median or sagittal section of a turtle skull. In this figure a series of structures are labeled which are relatively consistent in position throughout the *Chelonia* and are *not* labeled in the following series of median sections (figs. 67-80). However, to aid comparisons, the texture patterns used for the foramen nervi trigemini, hiatus acusticus, and foramen jugulare anterius are repeated in this series of median views. The specimen used here is the *Chrysemys concinna* illustrated in figure 78.

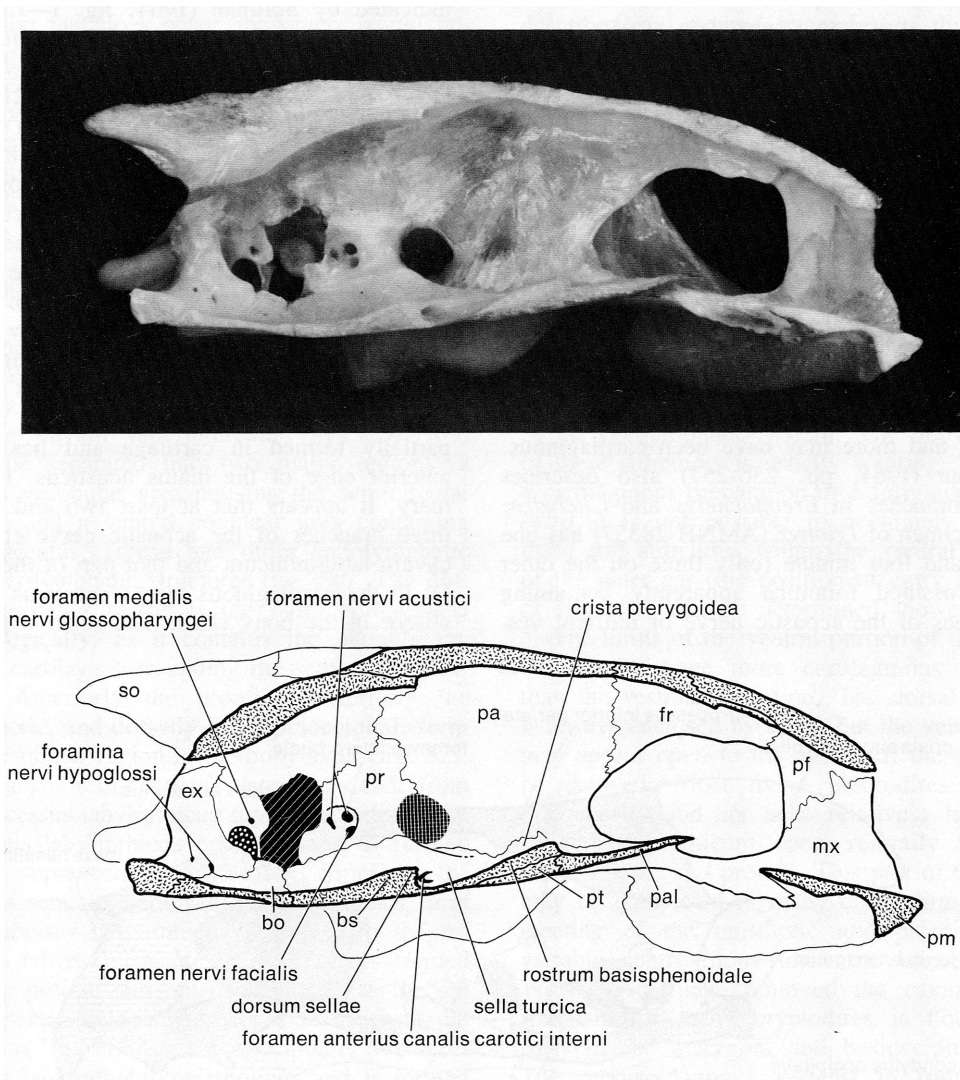


FIG. 67. *Pelusios subniger* (AMNH 71188, 32 mm.), Pelomedusidae, Maroantsetra, Malagasy Republic. Median section, cut areas indicated by irregular stipple. This section is on skull midline.

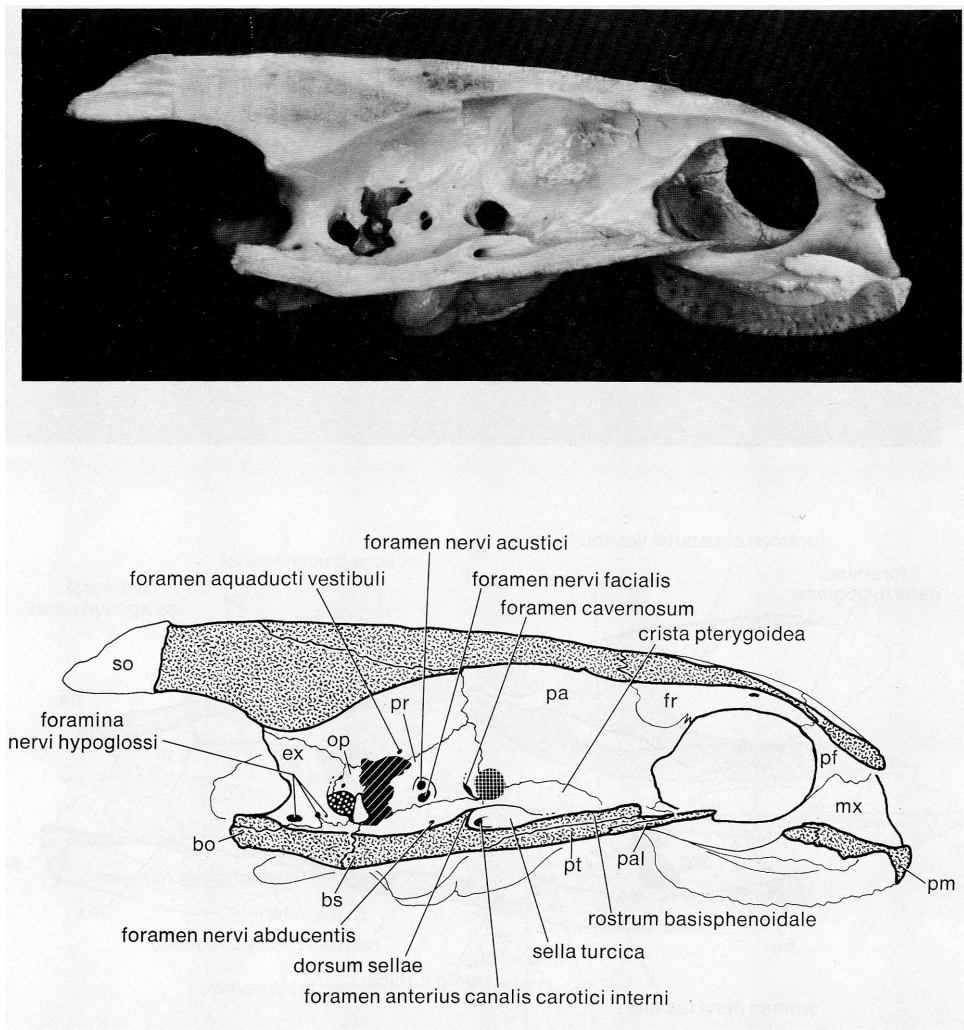


FIG. 68. *Podocnemis unifilis* (AMNH 58195, 64 mm.), Pelomedusidae, Iquitos, Loreto, Peru. Median section, cut areas indicated by irregular stipple. This section is on the midline of the skull.

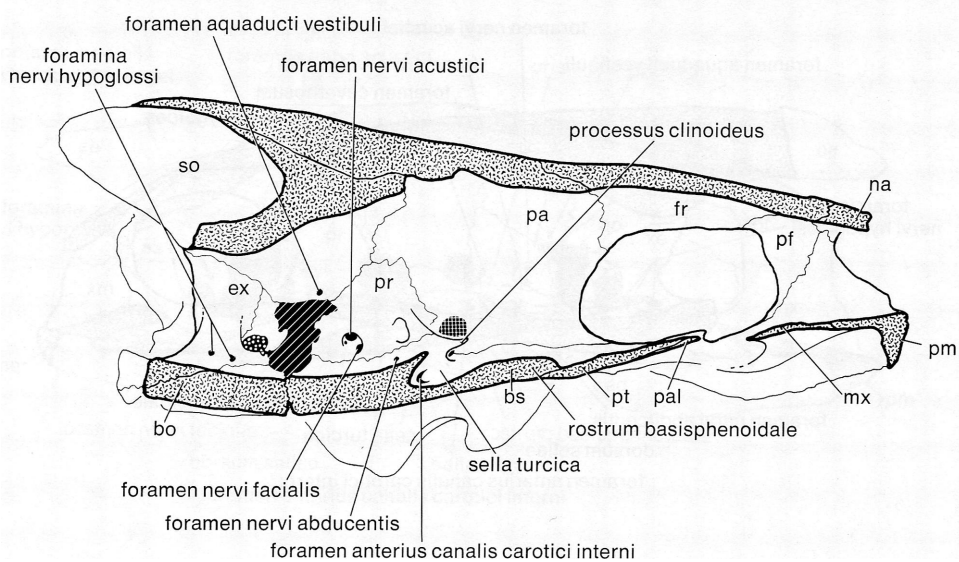


FIG. 69. *Emydura macquarrii* (AMNH 110487, 48 mm.), Chelidae, Cooper's Creek, South Australia, Australia. Median section, cut areas indicated by irregular stipple. This section is on skull midline. Right parietal is removed along suture exposing left parietal. Prootic forms a process not usually seen in turtles that reaches the basisphenoid.

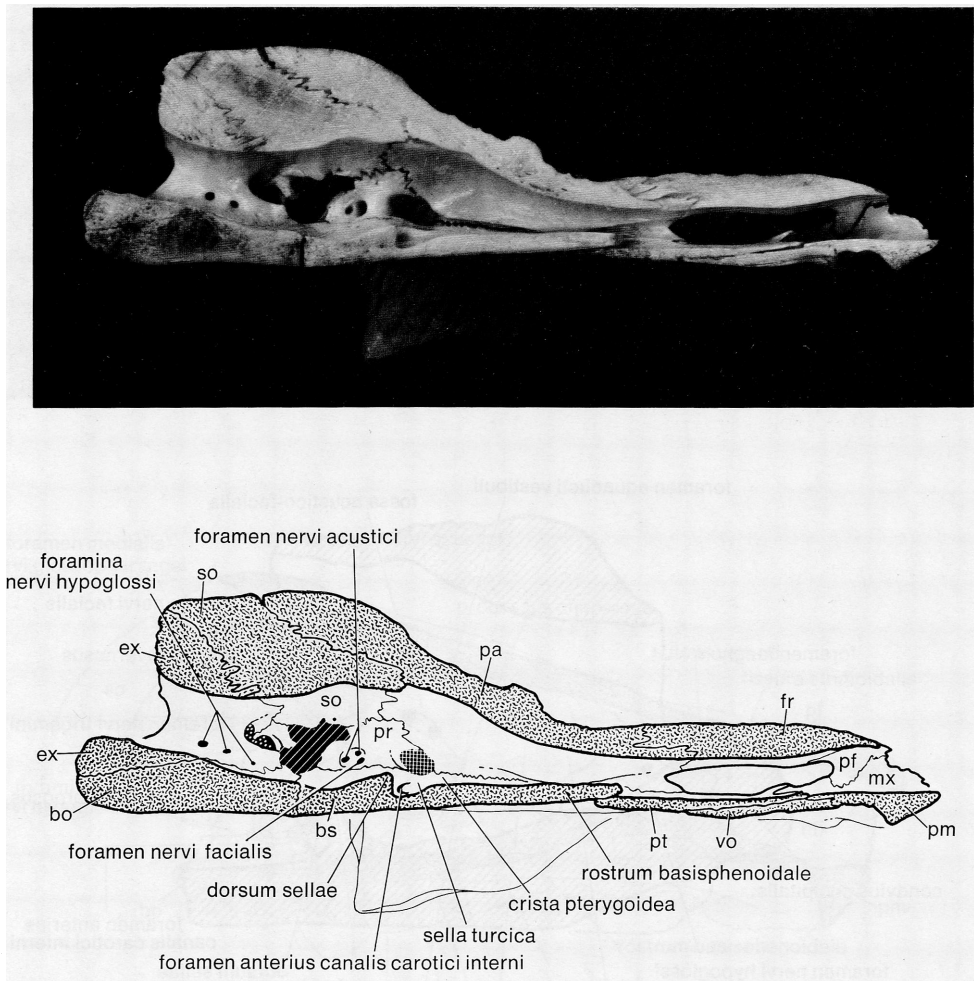


FIG. 70. *Chelus fimbriata* (AMNH 43298, 96 mm.), Chelidae, La Laquira Tejos Caicara, Venezuela. Median section showing right half of skull reversed to agree with other median sections figured here; cut area indicated by irregular stipple. Some of the bone between frontal and parietal broken. Section on skull midline.

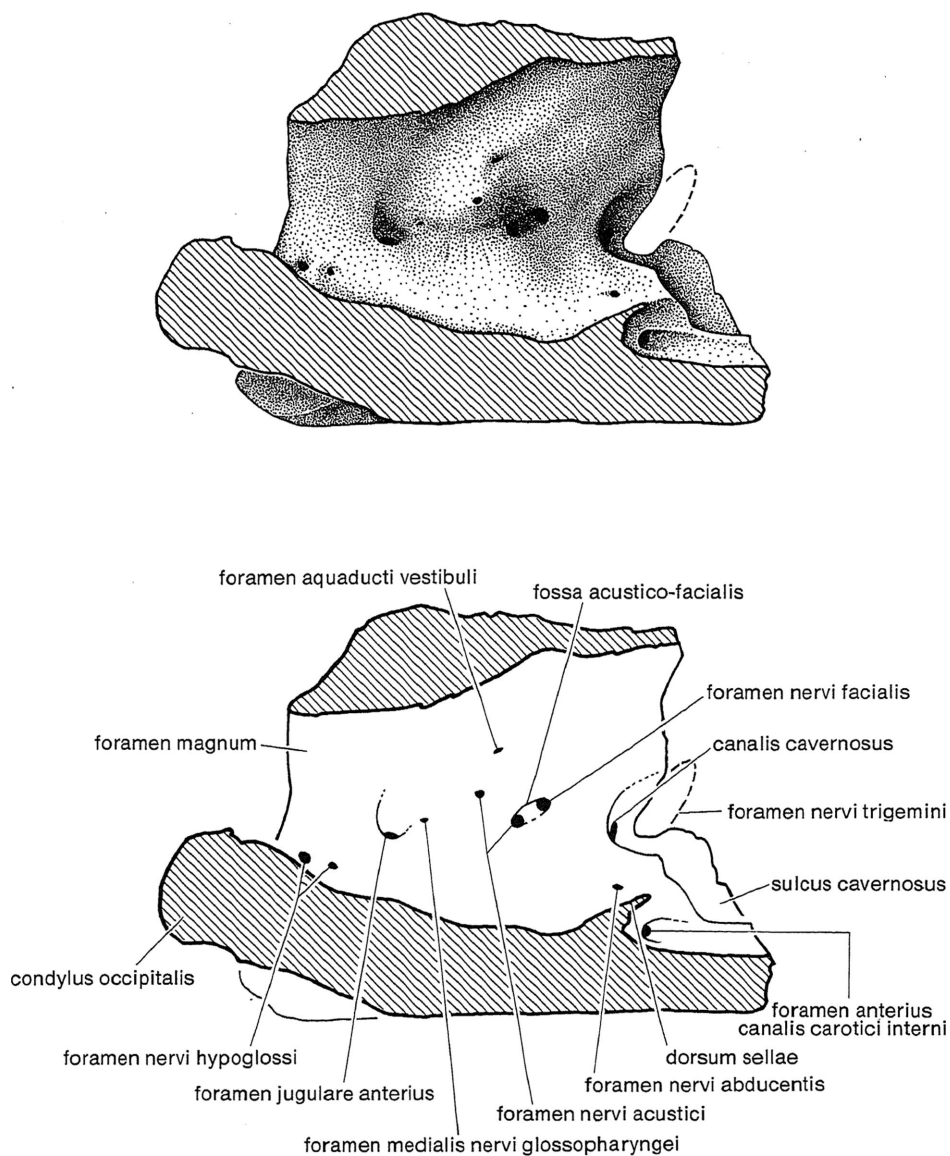


FIG. 71. *Baena arenosa* (YPM 3933, 28 mm.), Baenidae, Bridger Formation, Eocene, Grizzly Buttes, Wyoming. Median section through posterior part of skull, portion of skull anterior to foramen nervi trigemini missing. Irregular stipple indicates sectioned (or broken) surface.

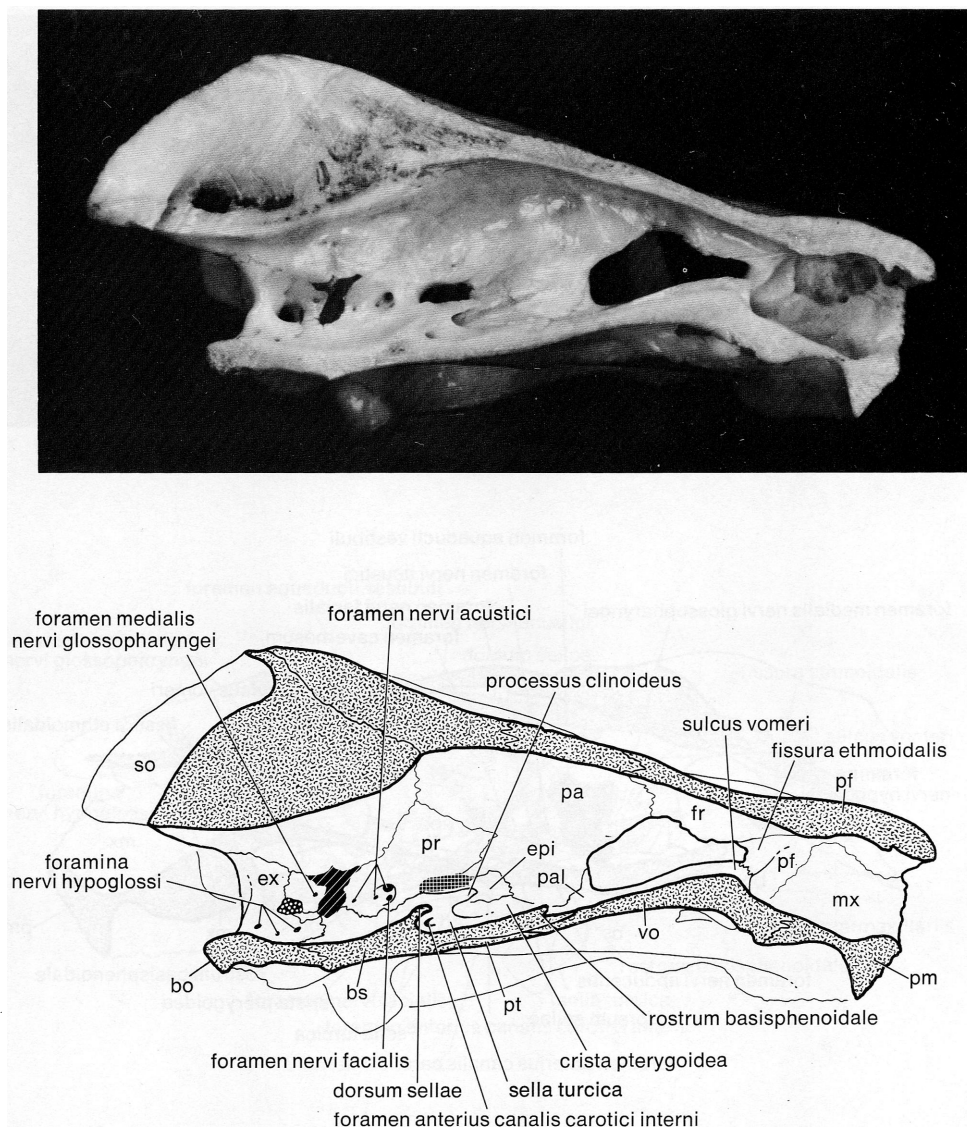


FIG. 72. *Sternotherus odoratus* (AMNH 69752, 36 mm.), Kinosternidae, Cotuit, Barnstable County, Massachusetts. Median section, cut area indicated by irregular stipple. Section is on the midline of the skull. Basioccipital-exoccipital suture indistinct.

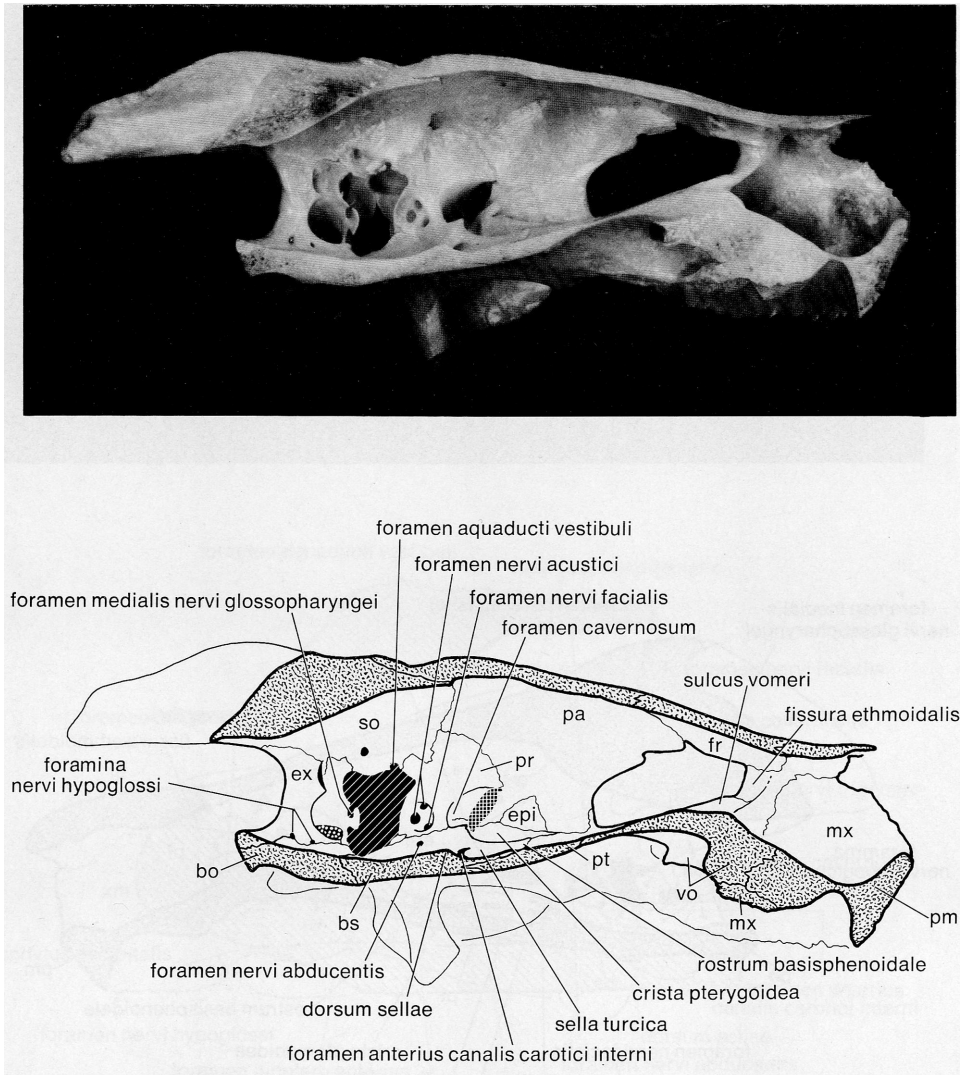


FIG. 73. *Dermatemys mawii* (MCZ 85551, 71 mm.), Dermatemydidae, Altar del Sacrificio on the Rio Ucamucinta, Mexico. Median section, cut area indicated by irregular stipple. This section is just slightly right of midline.

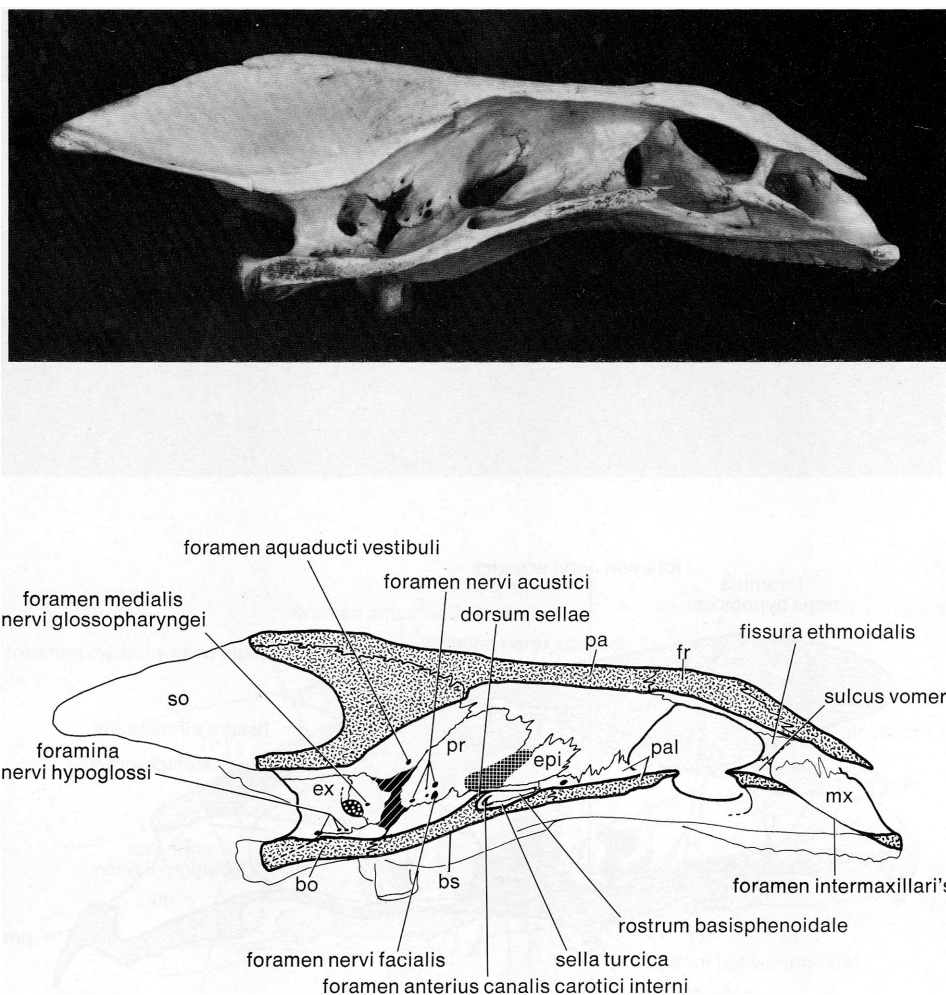


FIG. 74. *Trionyx ferox* (AMNH 57379, 96 mm.), Trionychidae, Lake Okeechobee, Okeechobee County, Florida. Median section, cut area indicated by irregular stipple. Section is slightly to the right of midline posteriorly and the premaxilla, a small nubbin in this group, is missing.

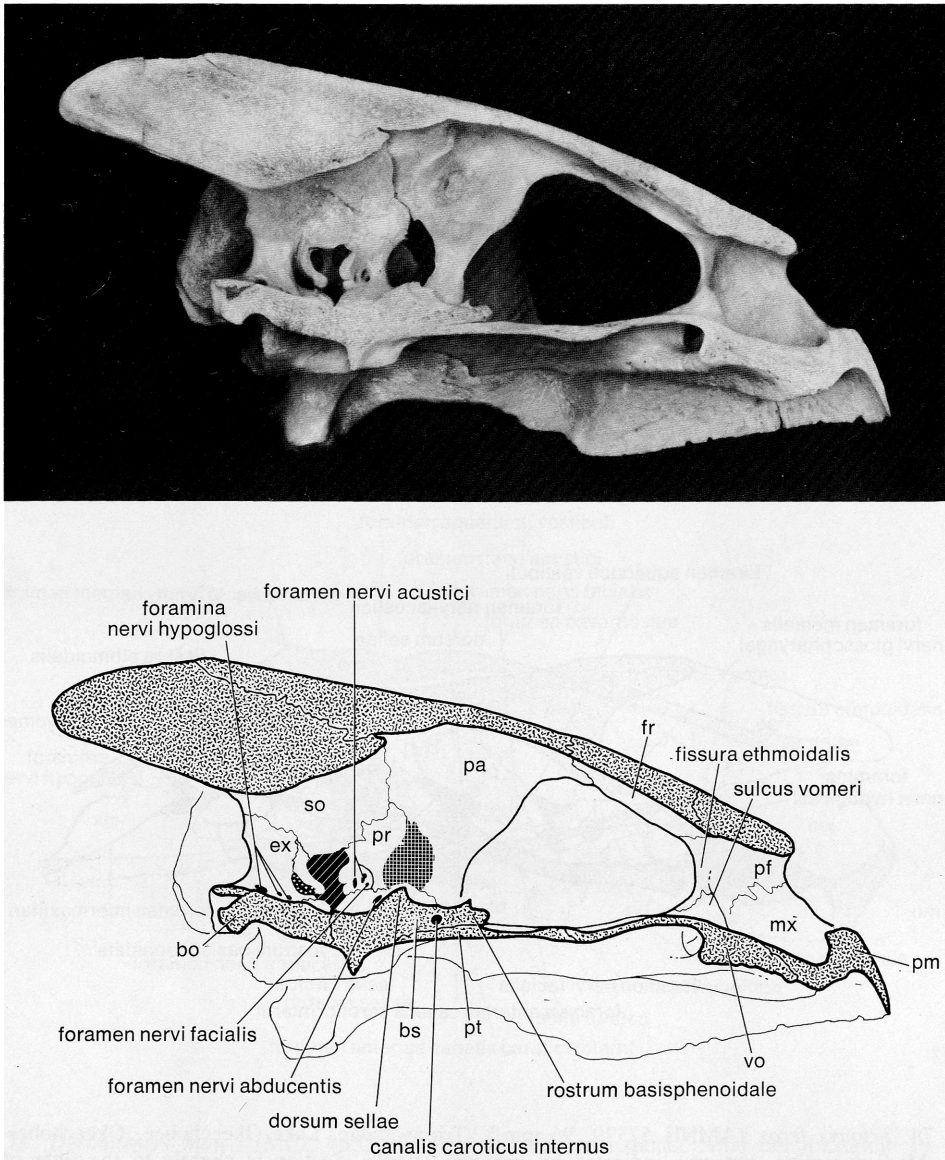


FIG. 75. *Eretmochelys imbricata* (AMNH 71599, 140 mm.), Cheloniidae, Daru, Papua. Median section, cut area indicated by irregular stipple. Section is cut slightly to the right of the midline missing the sella turcica and cutting the canalis caroticus internus just lateral to the sella turcica.

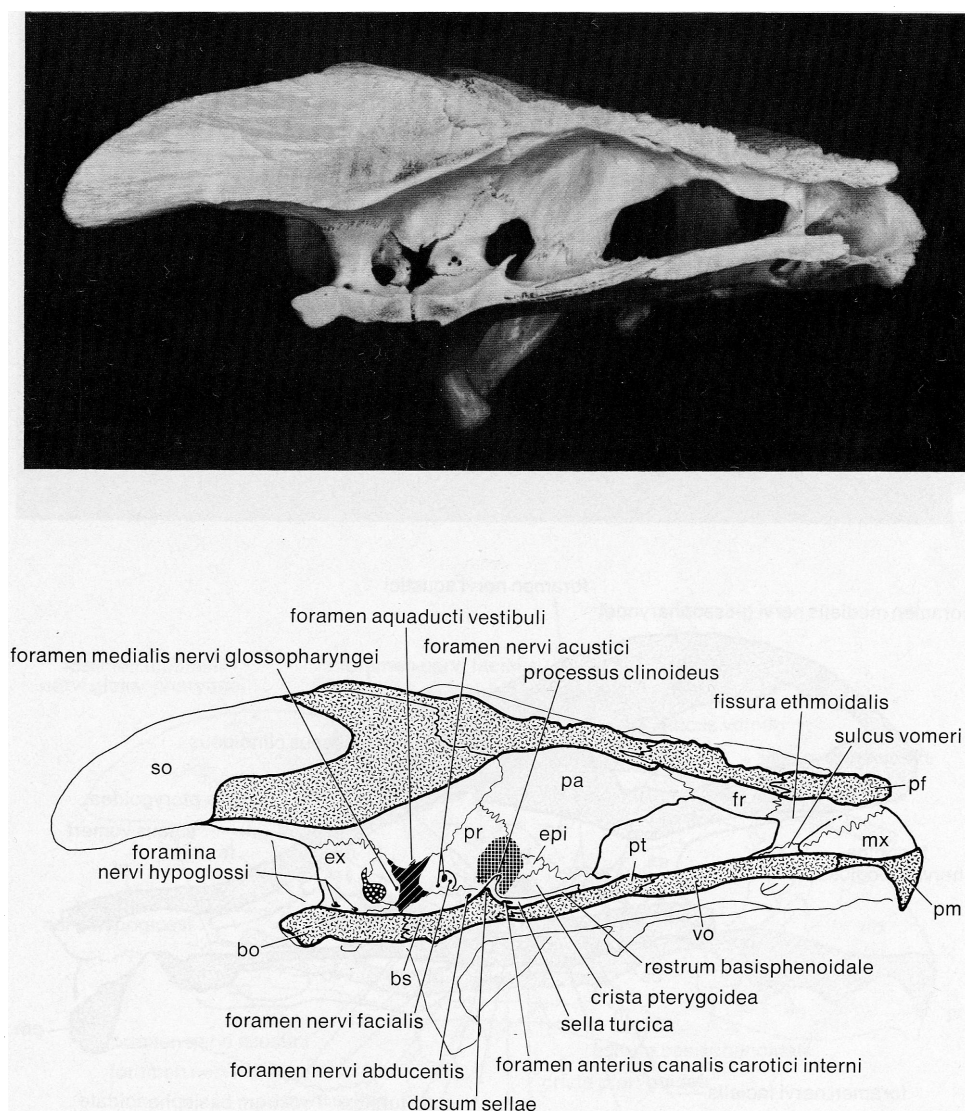


FIG. 76. *Chelydra serpentina* (AMNH 5305, 97 mm.), Chelydridae, no data. Median section, cut area indicated by irregular stipple. The section is on the midline but the rostrum basisphenoidale and a portion of the premaxilla were broken off and are restored in the labeled diagram.

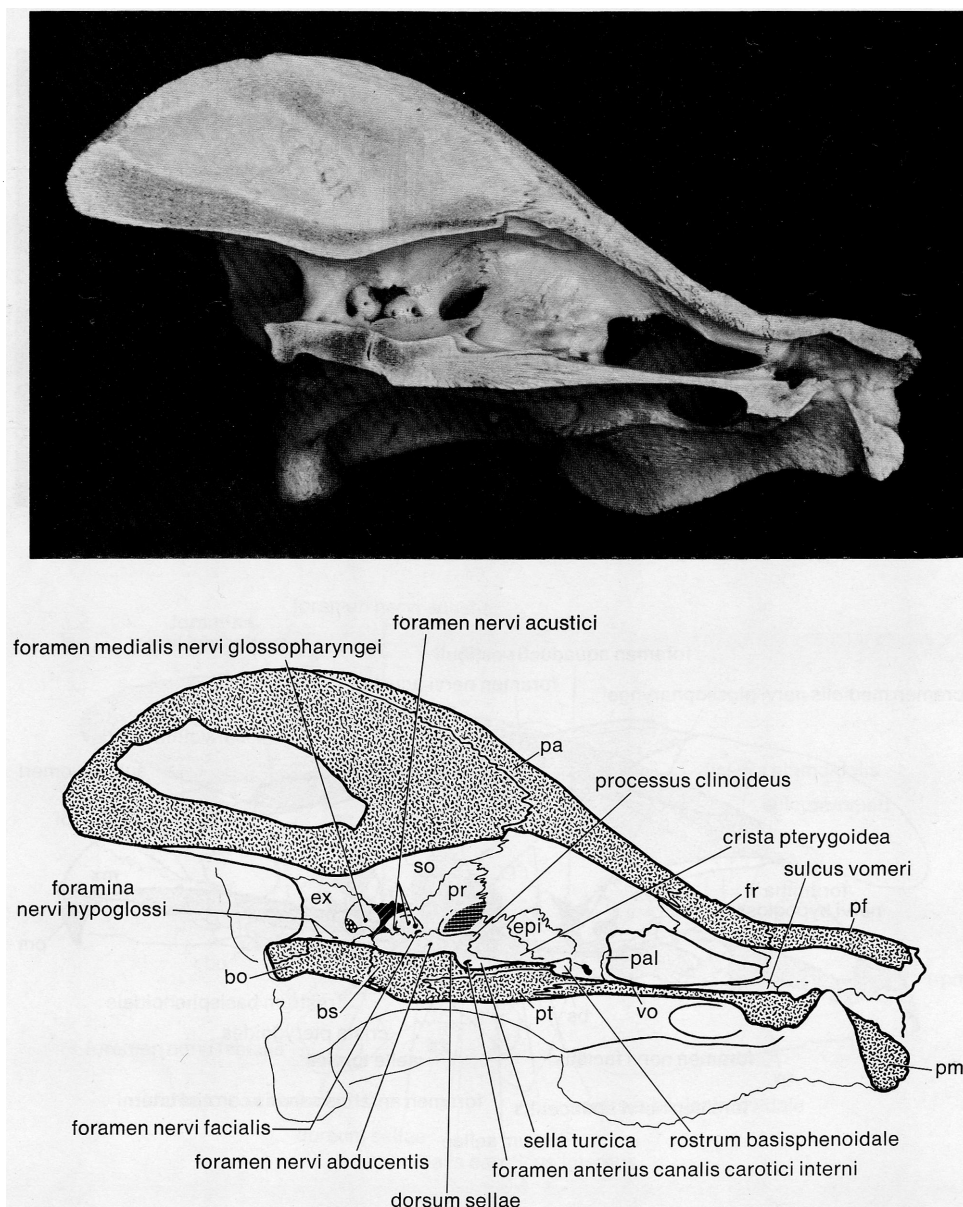


FIG. 77. *Macroclemys temminckii* (AMNH 7182, 162 mm.), Chelydridae, no data. Median section showing right half of skull reversed to agree with other median sections figured here, cut area indicated by irregular stipple. This section is on midline of skull. Unlabeled foramen in ventral area of processus inferior parietalis may contain the vidian nerve.

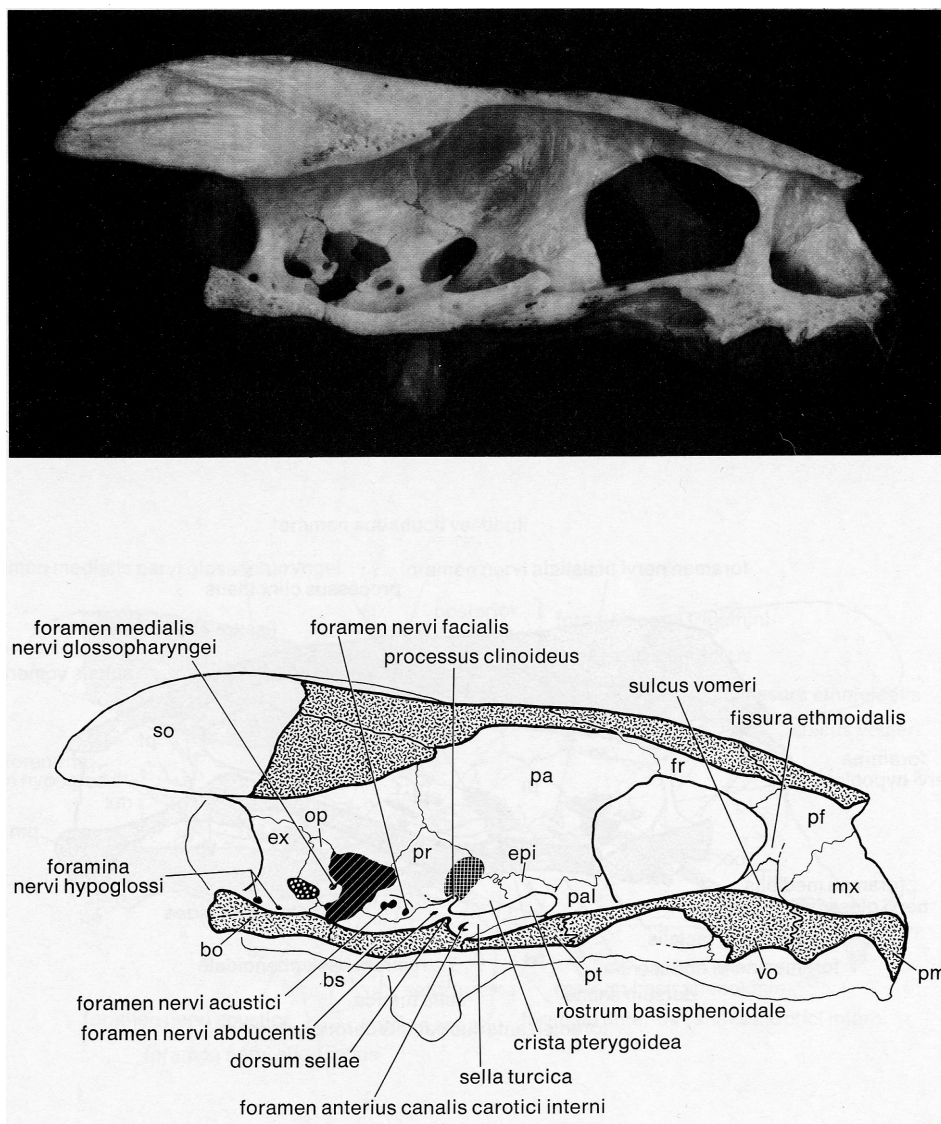


FIG. 78. *Chrysemys concinna* (AMNH 69914, 49 mm.), Emydidae, Eustis, Lake County, Florida. Median section, cut area indicated by irregular stipple. This section is in the midline of the skull.

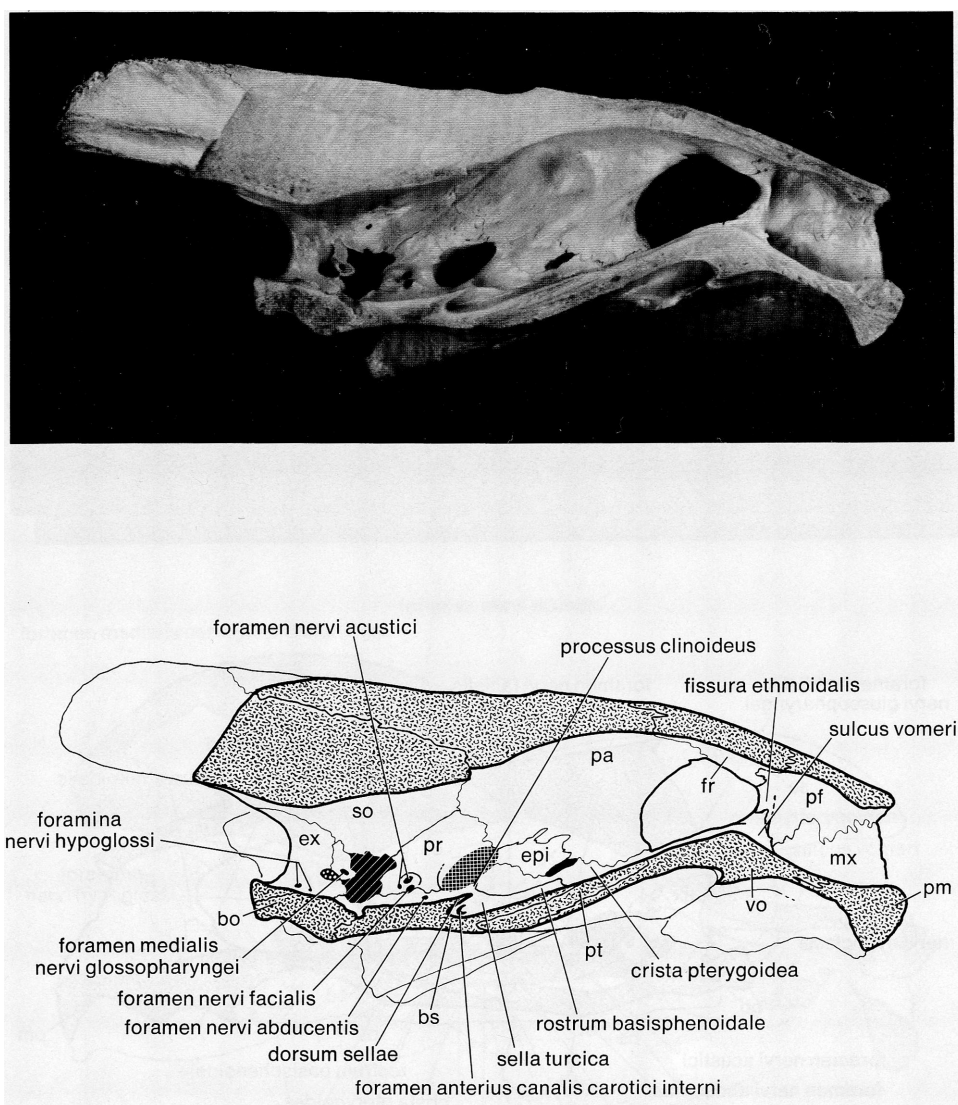


FIG. 79. *Chinemys reevesii* (AMNH 34223, 50 mm.), Emydidae, Fuching Hsien, Fukien Province, Peoples' Republic of China. Median section, cut area indicated by irregular stipple. Section is almost exactly in midline. "Foramen" between pterygoid and epipterygoid is due to breakage and was absent before sectioning.

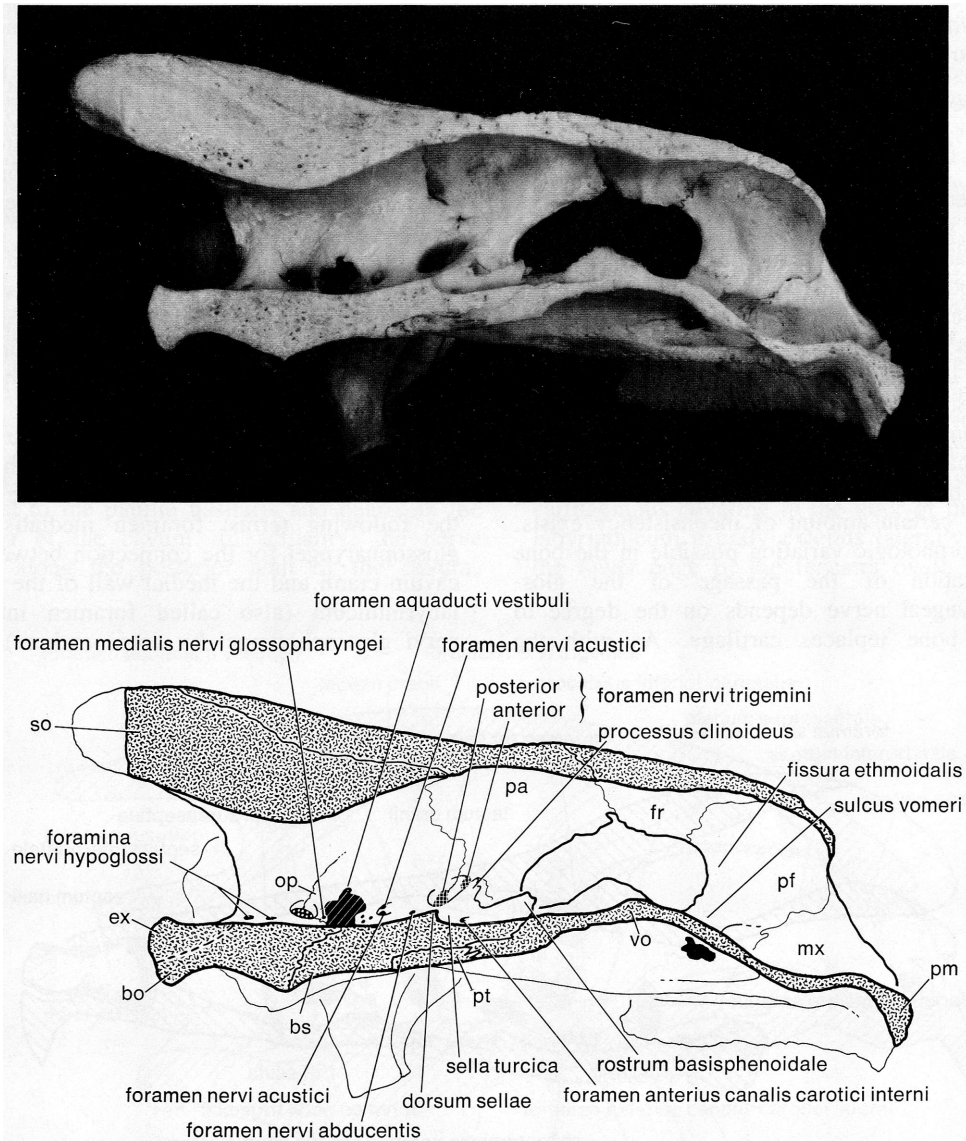


FIG. 80. *Geochelone elephantopus* (AMNH 87330, 97 mm.), Testudinidae, Duncan Island, Galapagos Islands. Median section, cut area indicated by irregular stipple. This section is slightly to the left of center anteriorly and slightly to the right of center posteriorly. Many of the neurocranial sutures are fused and no longer discernible. Note the division of the foramen nervi trigemini into two foramina.

of these foramina, particularly the cartilaginous ones, are not well known in a comparative sense, but at least one is usually closely associated with the facial (VII) nerve in the fossa acustico-facialis (Soliman, 1964, p. 256).

GLOSSOPHARYNGEAL NERVE FORAMINA

The other cranial nerve that penetrates the cavum labyrinthicum is the glossopharyngeal (IX) nerve. This nerve usually first enters the cavum through a cartilaginous foramen in the hiatus acusticus, although this may be ossified. As opposed to other vertebrates the nerve then either enters the cavum or (less commonly) remains buried in the posterior wall of the cavum labyrinthicum, that is, the processus interfenestralis. Most authors (Siebenrock, 1897, for example) have not differentiated the various foramina of the glossopharyngeal nerve and where they have differentiated them (Ogushi, 1911) a certain amount of inconsistency exists. The morphologic variation possible in the bone preservation of the passage of the glossopharyngeal nerve depends on the degree to which bone replaces cartilage. As with the

acoustic nerve and semicircular canals the situation is clearer in the fully developed chondrocranium (Kunkel, 1912). When the hiatus acusticus is well ossified a foramen can be seen in bone in the medial wall of the cavum labyrinthicum but when it is not well ossified none may be visible in the bony skull. More consistently, this nerve penetrates the processus interfenestralis forming a more medial and a more lateral foramen. Therefore, three foramina are possible. However, in the literature only two are usually named: an internal (or anterior) and an external (or posterior). The problem arises when the most medial foramen is actually in the hiatus acusticus and absent in the bony skull. In that case the next foramen actually in the processus interfenestralis is often given the same name as the absent foramen. In order to emphasize the variation that may exist I have suggested the use of the following terms: foramen medialis nervi glossopharyngei for the connection between the cavum cranii and the medial wall of the cavum labyrinthicum (also called foramen internum nervi glossopharyngei by some authors); fora-

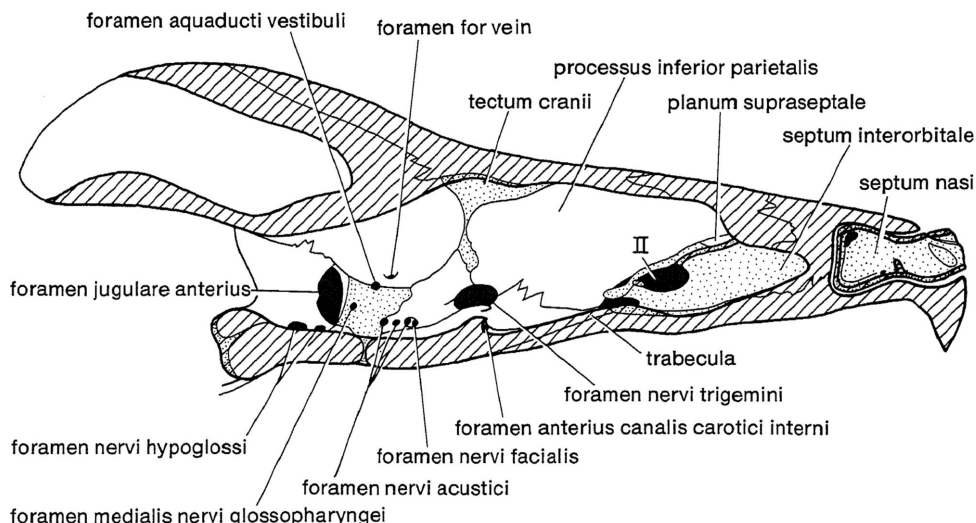


FIG. 81. *Chelydra serpentina*, Chelydridae. Median section, cut areas hatched, cartilage stippled. This figure shows the cartilaginous areas remaining in the adult. Modified from Nick (1912).

men internum nervi glossopharyngei for the opening from the cavum labyrinthicum into a canal in the processus interfenestralis of the opisthotic that leads to the foramen externum nervi glossopharyngei; and foramen externum nervi glossopharyngei for the external opening of the above described canal in the processus interfenestralis (this foramen opens into the cavum acustico-jugulare).

The passage of the glossopharyngeal nerve through the otic chamber has been noted by a number of workers as being quite different from other vertebrates (DeBurlet, 1934; Versluys, 1936; and references indicated by them). Versluys' figure 580, however, is somewhat misleading. The figure is diagrammatic and includes relationships that have been transposed from horizontal and vertical planes. In doing this, the glossopharyngeal nerve appears to cross the cavum labyrinthicum anterior and/or dorsal to the papilla basilaris and nearly in the center of the cavum. In actuality, the nerve runs along the posterior wall of the cavum,

sometimes within the bone, often within a groove, above the fenestra perilymphatica and does not extend into the central part of the cavum labyrinthicum.

AUDITORY STRUCTURES

The other openings of the cavum labyrinthicum are related to the auditory structures of the inner ear. The most prominent of these is the fenestra ovalis, formed between the cavum labyrinthicum and the cavum acustico-jugulare and containing the basis columellae or footplate of the columella auris. The fenestra ovalis is formed primarily by the prootic anteriorly and the opisthotic posteriorly. In the bony skull, the ventral margin appears to be formed by the pterygoid or, in many pleurodires, by nothing (it is open ventrally). However, the ventral margin is usually cartilaginous, and even in well-ossified skulls the cartilaginous covering in the floor of the cavum labyrinthicum usually extends laterally to form the lower edge of the fenestra ovalis. Species

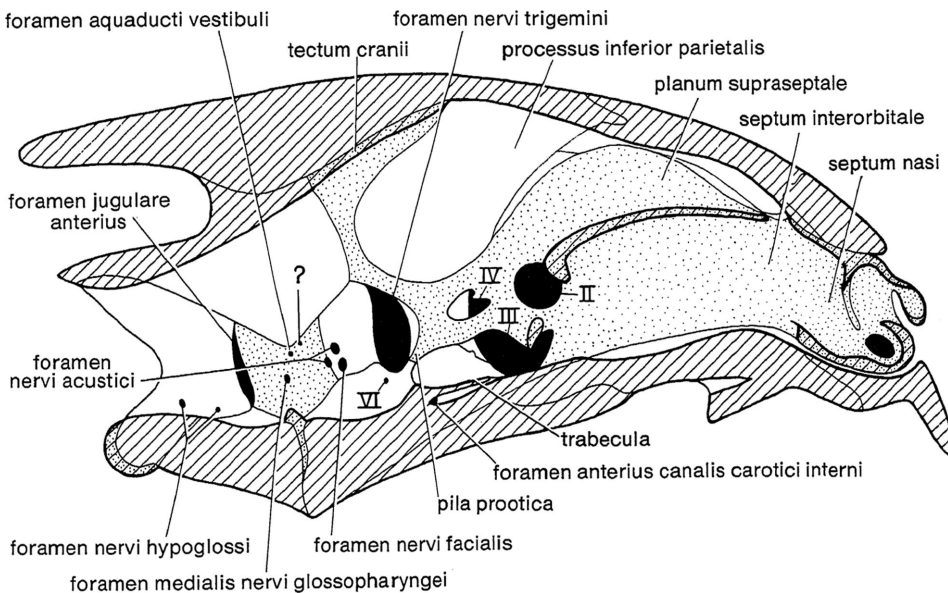


FIG. 82. *Chelonia mydas*, Cheloniidae. Median section, cut areas hatched, cartilage stippled. This figure shows the cartilaginous areas remaining in the adult. Modified from Nick (1912).

of *Trionyx* have a round foramen in the roof of the canalis caroticus internus in the pterygoid that directly underlies the fenestra ovalis (Ogushi, 1911, fig. 28), but I do not know if this is covered by cartilage or if it is open in life. Well-ossified individuals of *Chelydra serpentina* have a dorsally directed process of the pterygoid that abuts against the prootic and extends along the anterior edge of the fenestra ovalis. Pleurodires tend to have an irregular fenestra ovalis, and even in *Podocnemis expansa*, which has a process of the quadrate beneath the fenestra ovalis, a good deal of the opening is formed by cartilage.

Another prominent opening is the fenestra perilymphatica, connecting the cavum labyrinthicum with the cavum acustico-jugulare. It is formed primarily by the processus interfenestralis of the opisthotic but may be completed by the basioccipital or cartilage. The medial wall of the fenestra is usually formed by the opisthotic but in most living pleurodires it is cartilaginous. In many pleurodires the anterior wall of the foramen jugulare anterius is

also formed in cartilage and in the bony skull the fenestra perilymphatica is broadly continuous with the foramen jugulare anterius. The fenestra perilymphatica transmits the periotic sac (see Baird, 1960, 1970, and references indicated by him) from the inner ear into the recessus scalae tympani region of the cavum acustico-jugulare.

Another foramen penetrates the posterior wall of the cavum labyrinthicum in the vicinity of the fenestra perilymphatica; this is the hiatus postlagenum (see Cavum Acustico-jugulare).

The medial wall of the cavum labyrinthicum usually consists of a variable amount of cartilage persisting from the embryonic chondrocranium; the resulting space in the bony skull being termed the hiatus acusticus. Five bones make up the area surrounding the hiatus acusticus: basisphenoid anteroventrally, prootic anterodorsally, supraoccipital dorsally, opisthotic posterodorsally, and basioccipital posteroventrally. In the extinct Baenidae the hiatus acusticus is completely ossified with no indication of sutures.

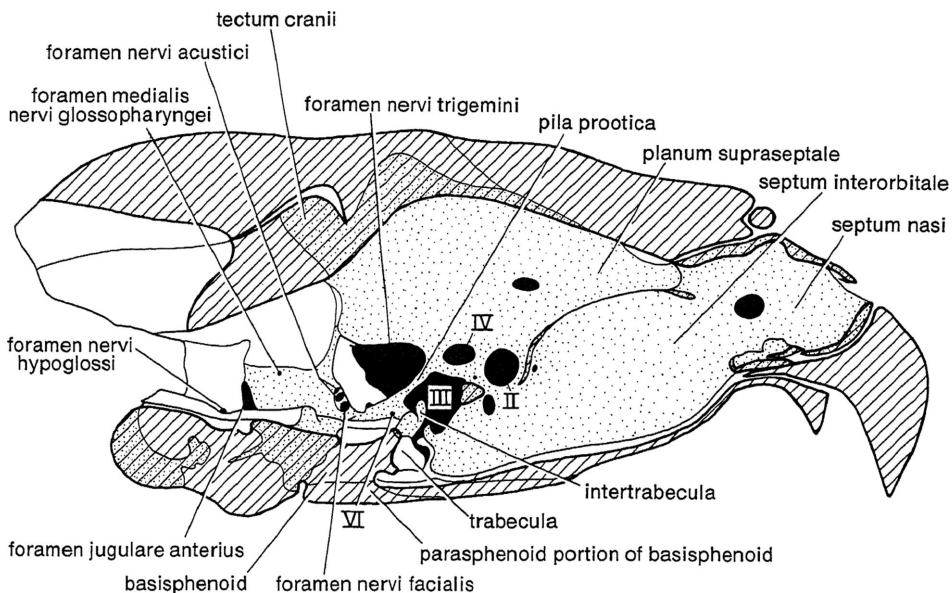


FIG. 83. *Dermochelys coriacea*, Dermochelyidae. Median section, cut areas hatched, cartilage stippled. This figure shows the cartilaginous areas remaining in the adult. Modified from Nick (1912).

A foramen named by Ogushi (1911, p. 21) the foramellum vasis vestibuli lies in the medial wall of the cavum labyrinthicum in the vicinity of the foramen aquaducti vestibuli. It transmits a vein and has only been reported in *Trionyx* (*ibid.*); however, I have seen similar minute foramina in *Caretta* and *Chelydra* and the foramen may be cartilaginous in other forms.

All but one of the foramina that penetrate the medial wall of the cavum labyrinthicum have been described above. This last foramen is the foramen aquaducti vestibuli which carries the endolymphatic duct from the sacculus to the endolymphatic sac in the cavum cranii. The foramen usually lies at the ventromedial edge of the supraoccipital, half being formed by bone and half by the cartilage in the hiatus acusticus. In some cases, however, all of the foramen may be formed in either bone or cartilage.

CAVUM ACUSTICO-JUGULARE

Figures 11, 12, 18, 19, 48, 50, 51, 84-102, 105-109

The cavum acustico-jugulare (figs. 50, 87) is an L-shaped space formed between the cavum labyrinthicum and the cavum tympani. It contains portions of the middle ear and various vessels and nerves. The morphology and structures of the cavum acustico-jugulare of turtles

are unique to this group and have features of taxonomic interest. The cavum acustico-jugulare may be divided into two sections based on its L shape. The longer arm of the L is here termed the cranioquadrate portion because it is a remnant of the cranioquadrate passage or space of Goodrich (1930, see below). It extends approximately anteroposteriorly and contains the vena capitis lateralis (lateral head vein) as a consistent landmark. The shorter arm of the L extends medially to lie behind the cavum labyrinthicum rather than mostly lateral as the larger section does. I am calling this smaller portion of the cavum acustico-jugulare the recessus scalae tympani (following DeBeer, 1937 and Baird, 1960), although it seems to be only partially homologous with the recessus scalae tympani of other reptiles (Baird, 1960, p. 932; see also below).

THE CRANIOQUADRATE SPACE PORTION OF THE CAVUM ACUSTICO-JUGULARE

The larger section of the cavum acustico-jugulare is the reduced equivalent of the cranioquadrate space of other vertebrates. The cranioquadrate passage or space is the area between the palatoquadrate elements and the primary neurocranium. Most reptile (as well as other vertebrate) embryos, many living lizards, and

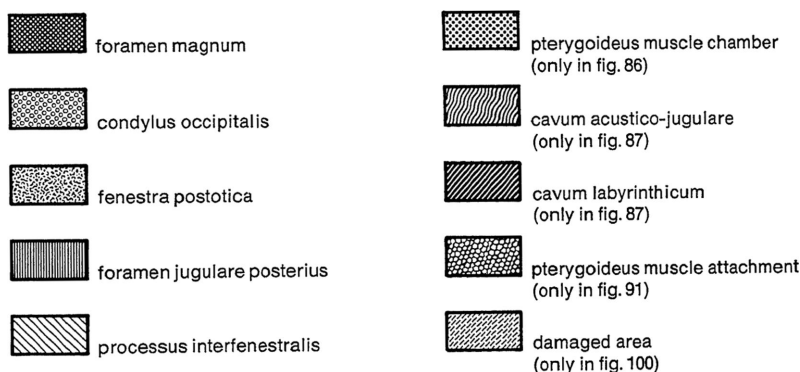


FIG. 84. Key to texture patterns used in middle ear stereophotographs (figs. 85-102) for ease of comparison and to reduce the number of labels. The left-hand column lists texture patterns found in nearly all the figures, whereas the patterns in the right-hand column occur in only a few figures. All but figure 87 of the following stereo-photographs are posteroventrolateral views of the right otico-occipital region.



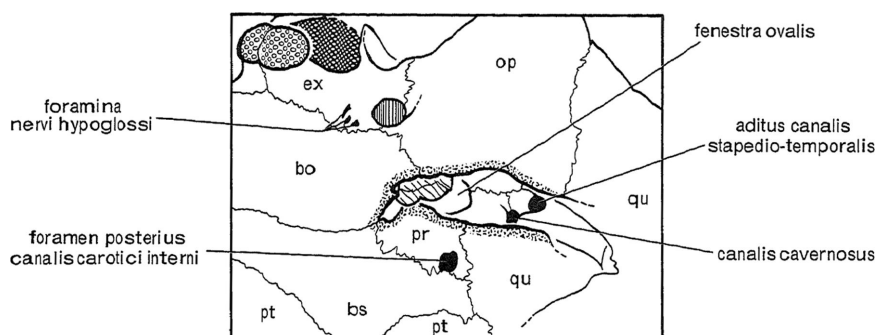


FIG. 85. *Pelusios* sp. (AMNH 10062, 55 mm.), Pelomedusidae, Faradje, Haut-Zaire, Zaire. A horizontally sectioned skull. See figure 84.

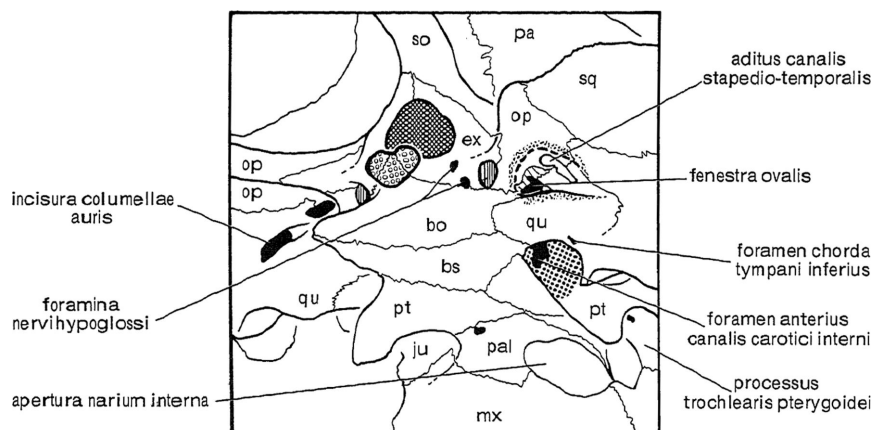


FIG. 86. *Podocnemis expansa* (AMNH 6823, 101 mm.), Pelomedusidae, no data. See fig. 84.

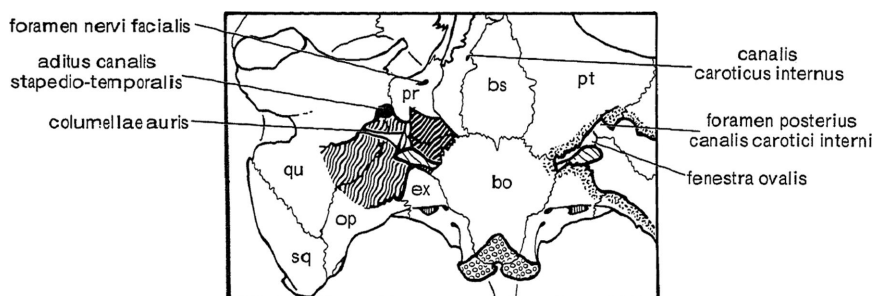
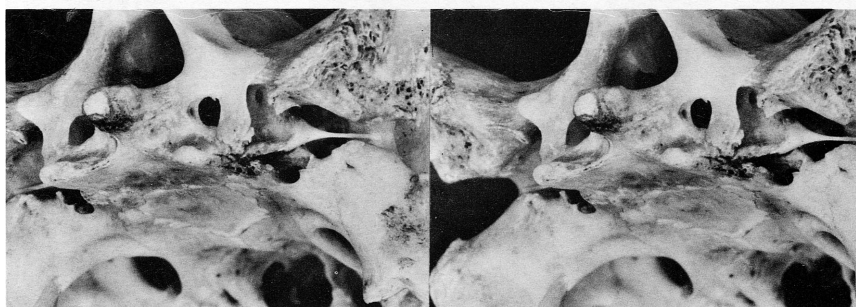
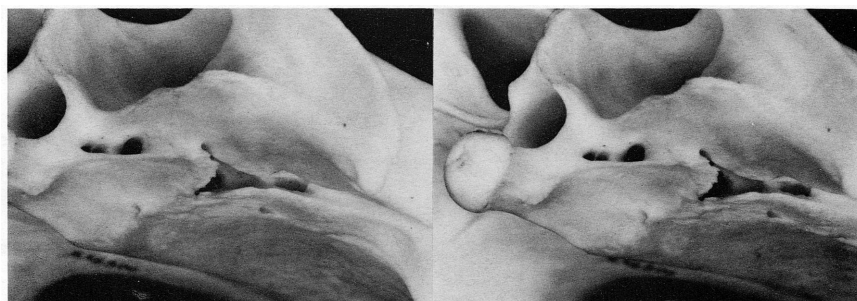


FIG. 87. *Chelydra serpentina* (AMNH 110446, 63 mm.), Chelydridae, no data. Ventral view of basicranium with right pterygoid removed. Left stapes missing. See figure 84.



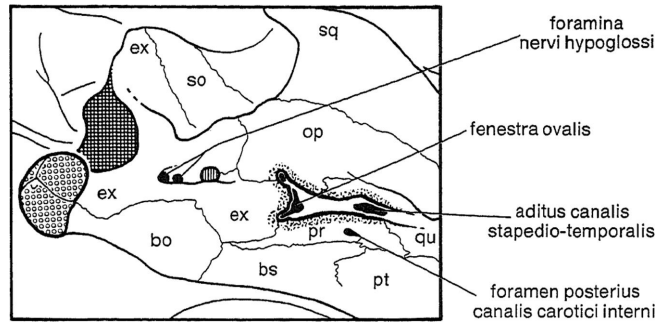


FIG. 88. *Chelus fimbriata* (AMNH 108955, 104 mm.), Chelidae, no data. See figure 84.

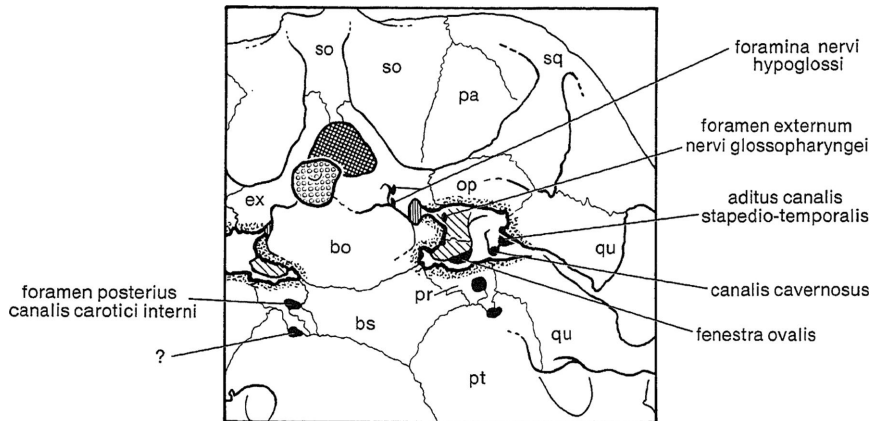


FIG. 89. *Pseudemydura umbrina* (Western Australian Museum, R 29341, 35 mm.), Chelidae, Twin Swamp Reserve, Western Australia. The contents of the foramen marked "?" are unknown to me. See figure 84.

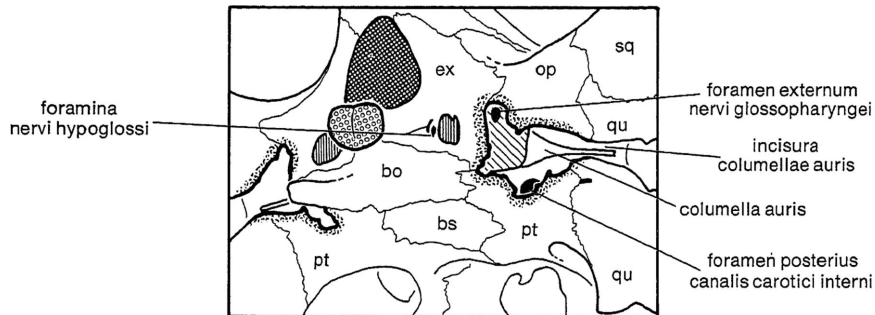
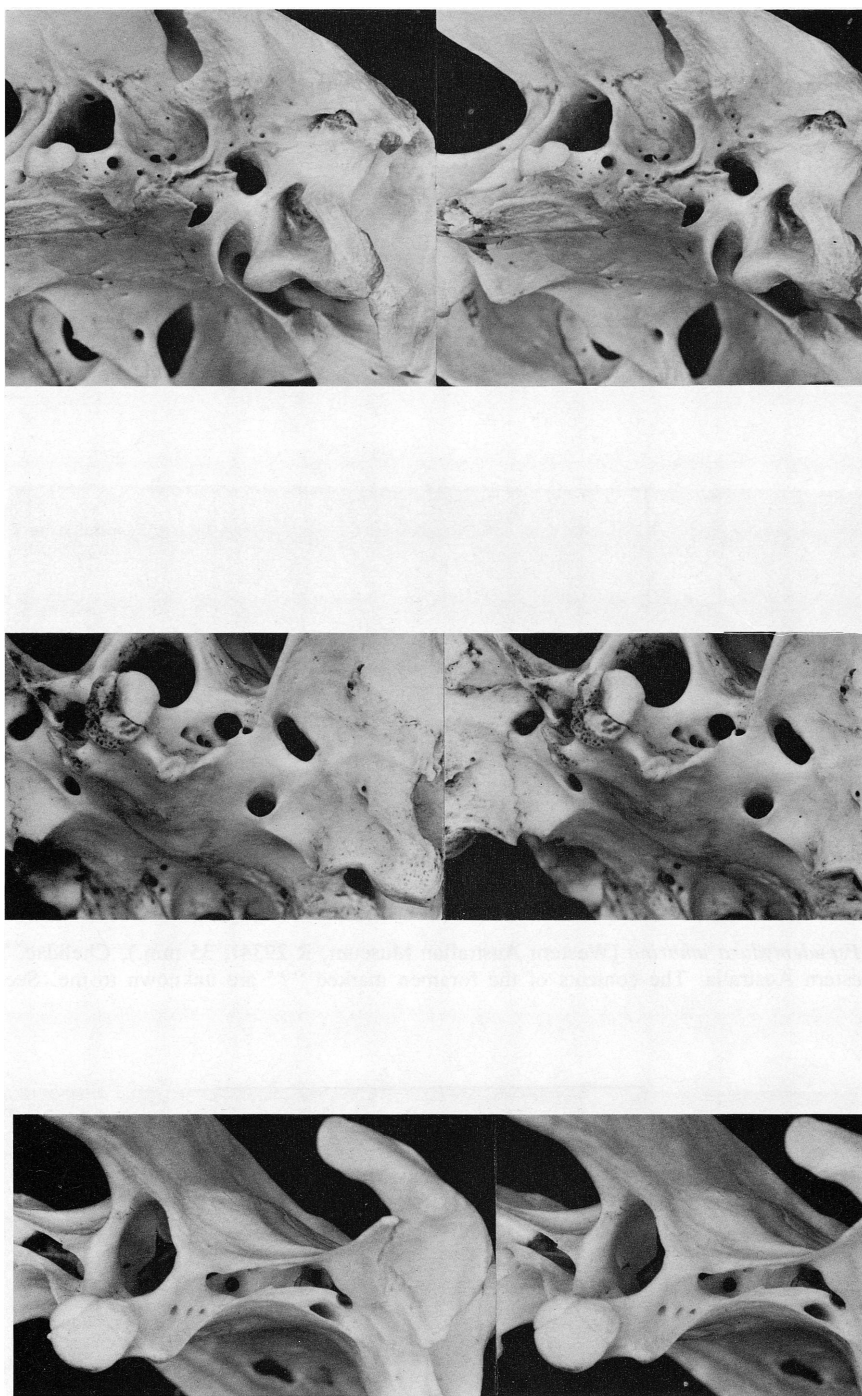


FIG. 90. *Dermatemys mawii* (NMNH 66669, 73 mm.), Dermatemydidae, "Tehuantepec," Mexico. See figure 84.



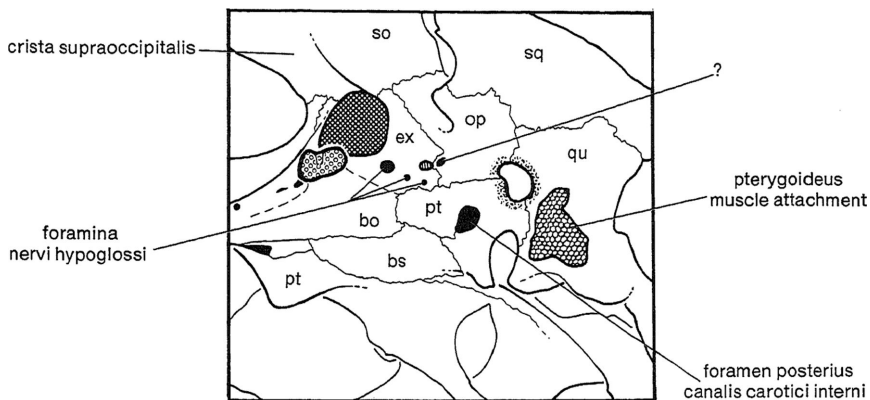


FIG. 91. *Carettochelys insculpta* (AMNH 84212, 101 mm.), *Carettochelyidae*, Fly River, Papua. See figure 84.

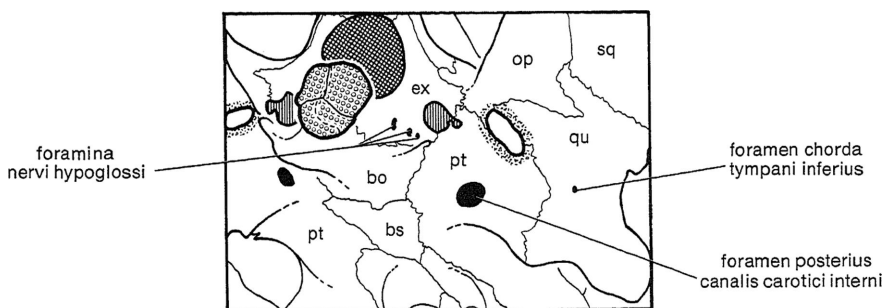


FIG. 92. *Cyclanorbis senegalensis* (MCZ 42599, 75 mm.), *Trionychidae*, Gabon. See figure 84.

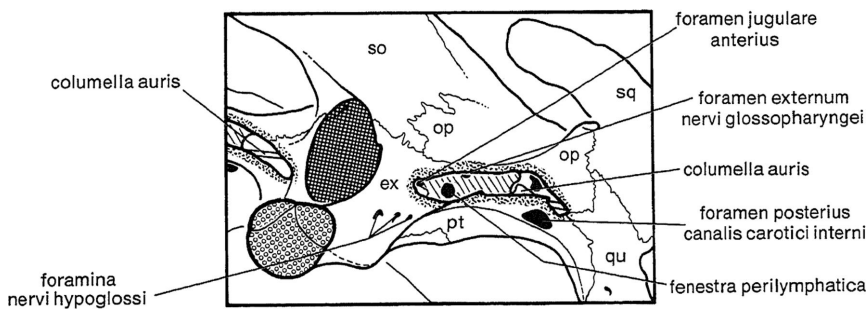


FIG 93. *Pelochelys bibroni* (AMNH 23541, 85 mm.), *Trionychidae*, Nodda, Hainan Island, Kwangtung Province, Peoples' Republic of China. See figure 84.



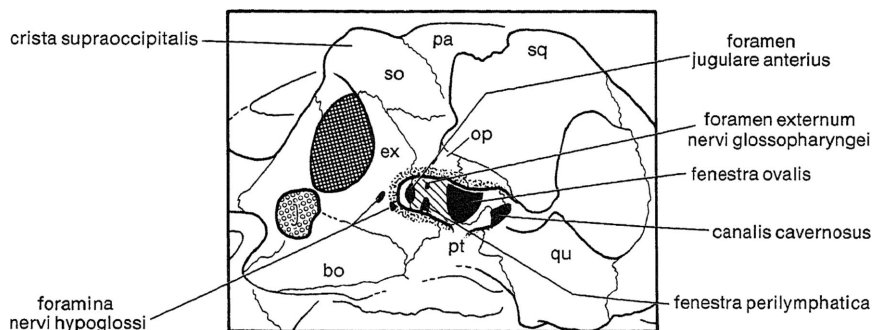


FIG. 94. *Chisternon undatum* (AMNH 5961, 68 mm., estimated), Baenidae, Bridger Formation, Eocene, Grizzly Buttes West, Wyoming. See figure 84.

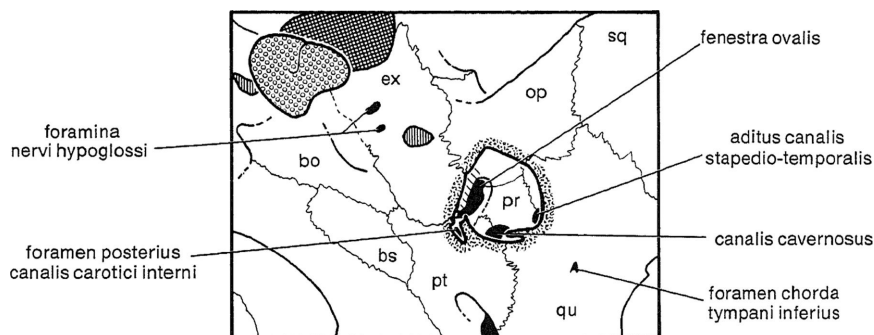


FIG. 95. *Chelydra serpentina* (AMNH 67092, 102 mm.), Chelydridae, Bronxville, Westchester County, New York. See figure 84.

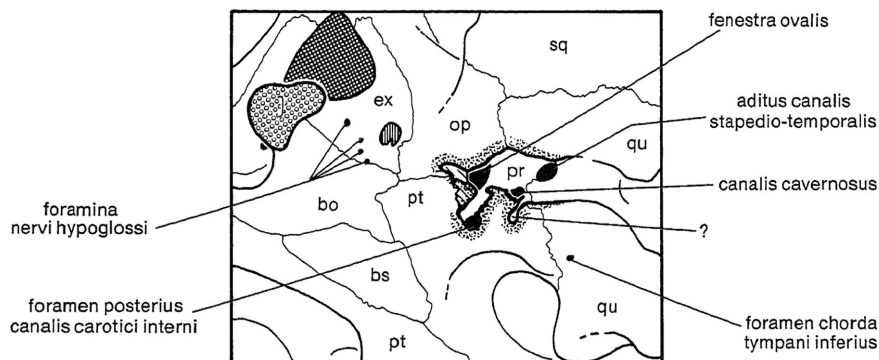


FIG. 96. *Batagur baska* (NMNH 29483, 94 mm.), Emydidae, Indragiri R., Sumatra, See figure 84.



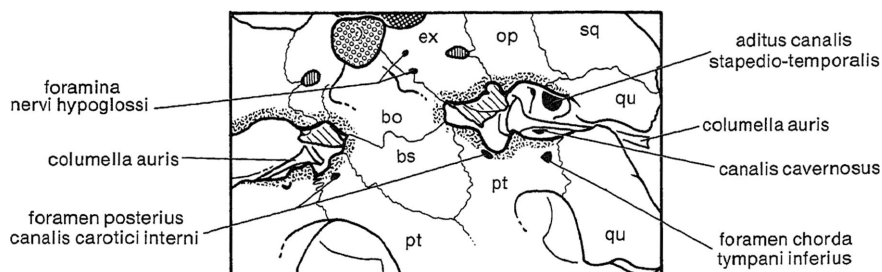


FIG 97. *Chrysemys concinna* (AMNH 111960, 44 mm.), Emydidae, Colorado River, Travis County, Texas. See figure 84.

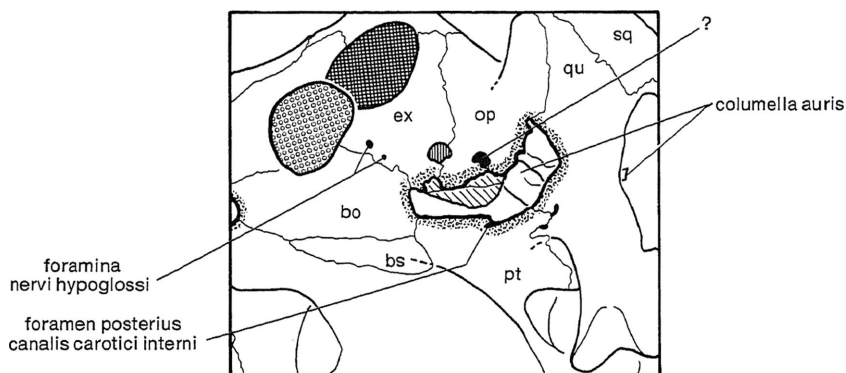


FIG. 98. *Gopherus polyphemus* (AMNH 73815, 44 mm.), Testudinidae, Silver Springs, Marion County, Florida. See figure 84.

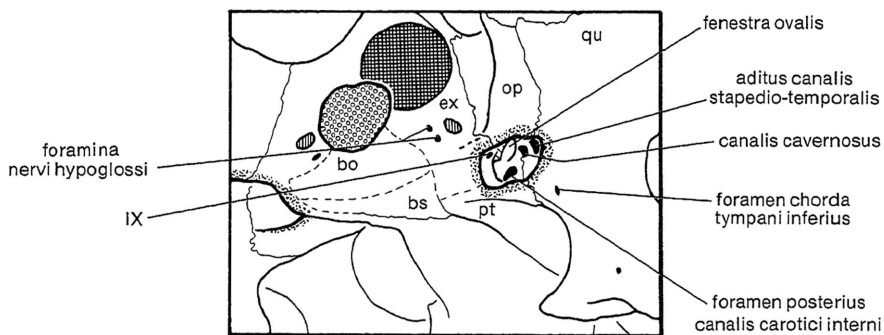
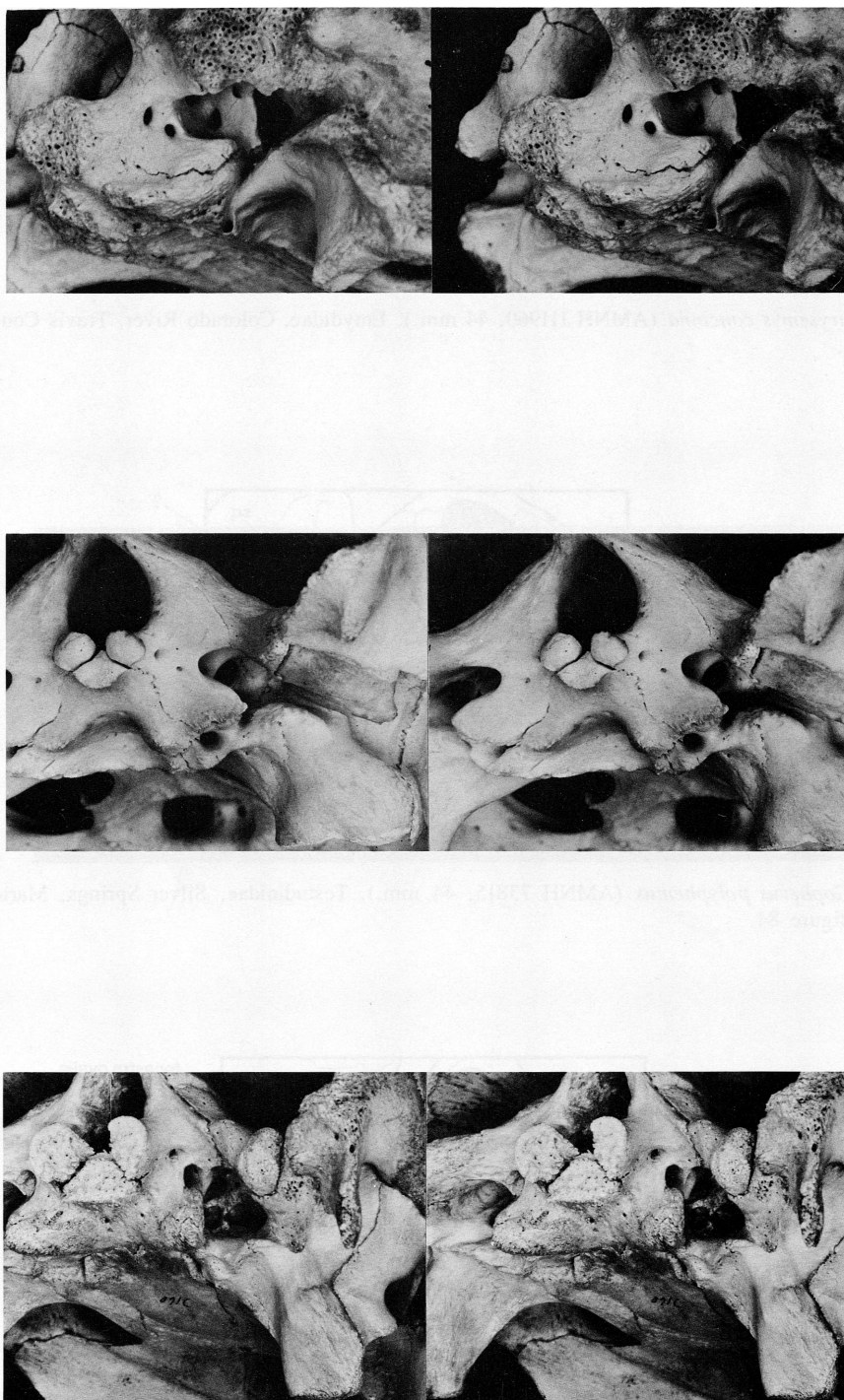


FIG. 99. *Geochelone elephantopus* (AMNH 64019, 97 mm.), Testudinidae, Galapagos Islands. See figure 84.



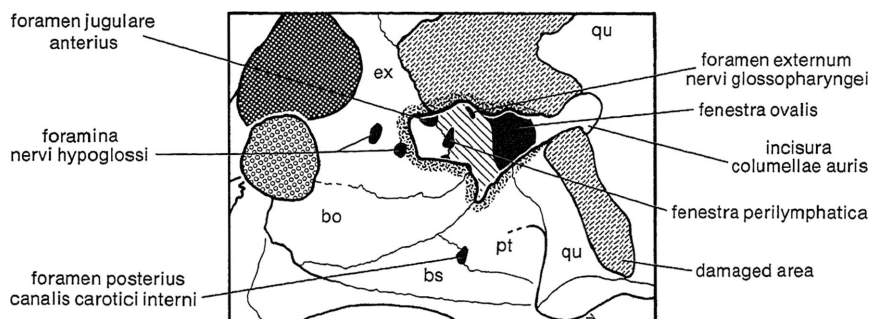


FIG. 100. *Plesiochelys etalloni* (SM 134, midline length as preserved 62 mm.), Plesiochelyidae, Late Jurassic, Solothurn, Switzerland. See figure 84.

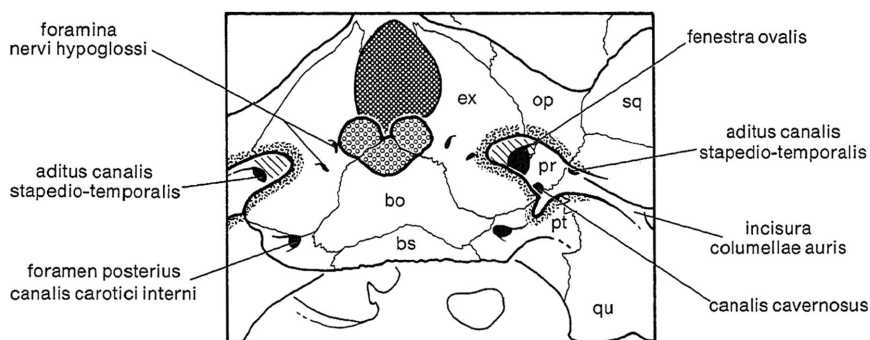


FIG. 101. *Lepidochelys olivacea* (FMNH 31334, 107 mm.), Cheloniidae, Crystal River, Florida. See figure 84.

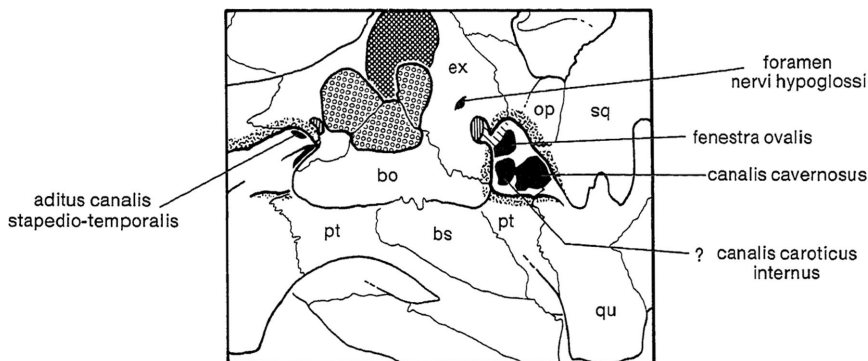


FIG. 102. *Dermochelys coriacea* (AMNH 7160, 229 mm.), Dermochelyidae, no data. See figure 84.

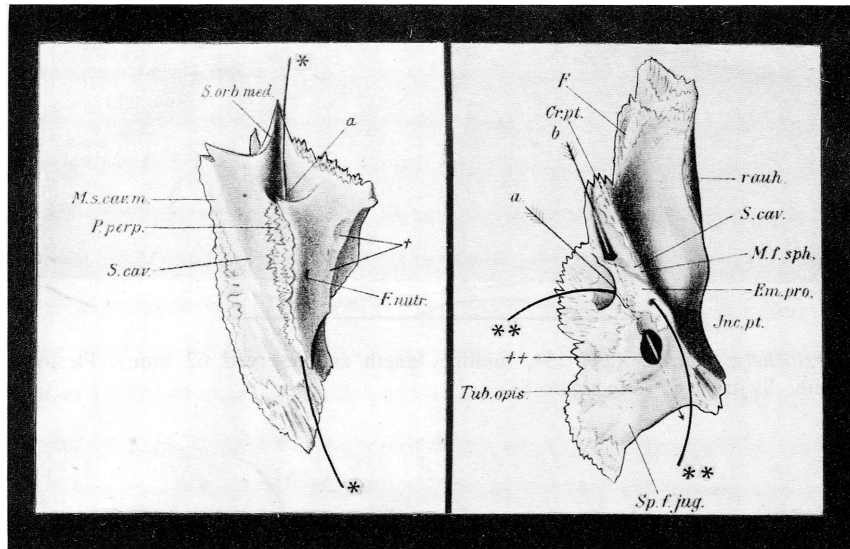


FIG. 103. *Trionyx sinensis* (*T. japonicus*), Trionychidae. Left, dorsal view of right palatines; right, dorsal view of right pterygoid. Anterior toward top of page.

Abbreviations for left-hand figure: a., foramen palatinum posterius; F. nutr., ?nutritive foramen; M. s. cav. m., medial margin of sulcus cavernosus; P. perp., dorsal process of palatine; S. cav., sulcus cavernosus; S. orb. med., posterior margin of foramen orbito-nasale; + pterygoid attachment area; *——* canalis nervi vidiani (posterior opening is foramen nervi vidiani).

Abbreviations for right-hand figure (see also fig. 25): a., arrow going through canalis caroticus internus; b., arrow following course of mandibular artery through the foramen caroticum laterale and into the canalis caroticus internus; Cr. pt., crista pterygoidea; Em. pro., prootic attachment on crista pterygoidea; F., I do not know; Inc. st., I don't know; M. f. sph., foramen nervi trigemini; rauh., processus pterygoideus externus; S. cav., sulcus cavernosus; Sp. f. jug., floor of cavum acustico-jugulare; Tub. opis., attachment area for processus interfenestralis of opisthotic; **——** path of VII nerve through foramen pro ramo nervi vidiani; ++ unossified portion of roof of canalis caroticus internus; cartilaginous in life. After Ogushi, 1911.

primitive reptiles such as *Captorhinus* (Romer, 1956, fig. 36) have a palatoquadrate that is free from the neurocranium and articulates with it via a basiptyergoid articulation (or, in embryos, a palatobasal articulation; see Goodrich, 1930, p. 423). Goodrich (*ibid.*, especially figs. 263, 449, 493) and DeBeer (1937) described the vessels and nerves that lie between the palatoquadrate and neurocranium in the cranioquadrate passage. In turtles the basiptyergoid articulation is fused and the area of the cranioquadrate passage is nearly obliterated by the broad sutural contact of the primary braincase (prootic and opisthotic) and quadrate, pterygoid and, when present, epiptyergoid. The soft structures that may be used to identify this area are described by Goodrich (1930) and are as follows: the vena capitis lateralis (lateral head vein), the

arteria stapediais (stapedial artery), and the hyomandibular branch of the facial (VII) nerve. In an embryonic *Emys orbicularis* these structures and the cranioquadrate space can be identified and followed during development (Kunkel, 1912; Shaner, 1926). In an adult turtle this area is represented by the larger, lateral portion of the cavum acustico-jugulare where the above-mentioned soft structures may be found.

The arteria stapediais enters the skull via the fenestra postotica (sometimes restricted by partitions, see fenestra postotica below), after branching off the main stem of the internal carotid artery. In kinosternids and trionychids the stapedial artery is reduced or vestigial (McDowell, 1961; Albrecht, 1967; Gaffney 1975d) compared to the internal carotid,

whereas in most other turtles the carotid is smaller than the stapedia. This results in the structures (described below) containing the stapedia artery varying in size relative to the internal carotid artery in these groups. The stapedia artery may be absent, as in *Dermatemys*, and then the structures containing it are absent. The stapedia artery travels anteriorly along the top of the cavum acustico-jugulare until it reaches the aditus canalis stapedio-temporalis. At this point in most cryptodires the arteria mandibularis (mandibular artery; also called the facial artery by some authors) continues forward in the canalis cavernosus until it exits via the foramen nervi trigemini. In pleurodires the

mandibular artery branches off the stapedia after the latter exits from the skull and enters the fossa temporalis superior. The aditus canalis stapedio-temporalis is formed by the quadrate laterally and the prootic medially. The stapedia artery turns anterodorsally to continue between these two bones in the canalis stapedio-temporalis and enters the fossa temporalis superior by way of the foramen stapedio-temporale. These structures containing the stapedia artery are absent in *Dermatemys* and *Baptemys* and reduced in kinosternids. The vena capitis lateralis (lateral head vein) also enters the skull via the fenestra postotica. It then runs anteriorly, usually beneath the stapedia artery, and then

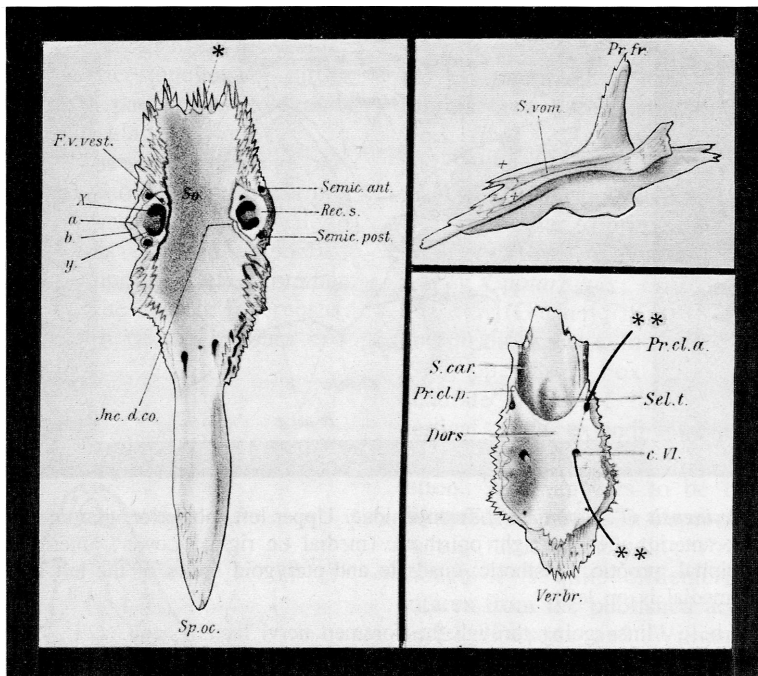


FIG. 104. *Trionyx sinensis* (*T. japonicus*), Trionychidae. Left, ventral view of supraoccipital (anterior toward top of page); right upper, posterolateral view of vomer (anterior on left); right lower, dorsal view of basioccipital (anterior toward top of page).

Abbreviations: a. and b., region of cavum labyrinthicum; c. VI., posterior opening of foramen nervi abducentis (the line goes through the entire foramen nervi abducentis); Dors., dorsum sellae; F. v. vest., "foramellum vasis vestibuli" of Ogushi, 1911; Inc. d. co., foramen aqueducti vestibuli; Pr. cl. a., rostrum basisphenoidale; Pr. cl. p., processus clinoides; Pr. f., paired dorsolateral processes that articulate with prefrontals; Rec. s., recessus labyrinthicus supraoccipitalis; S. car., sulcus for carotid artery; Sel. t., sella turcica; Semic. ant., canalis semicircularis anterior; Semic. post., canalis semicircularis posterior; Sp. oc., crista supraoccipitalis; S. vom., sulcus vomeri; Verbr., I don't know; X., canalis semicircularis anterior; Y., canalis semicircularis posterior; * portion of supraoccipital often remaining cartilaginous through maturity; *—* canalis abducentis; + palatine attachment area. After Ogushi, 1911.

into the canalis cavernosus. The canalis cavernosus (see Pterygoid) begins in the anterior

wall of the cavum acustico-jugulare and continues anteriorly, usually being formed by the

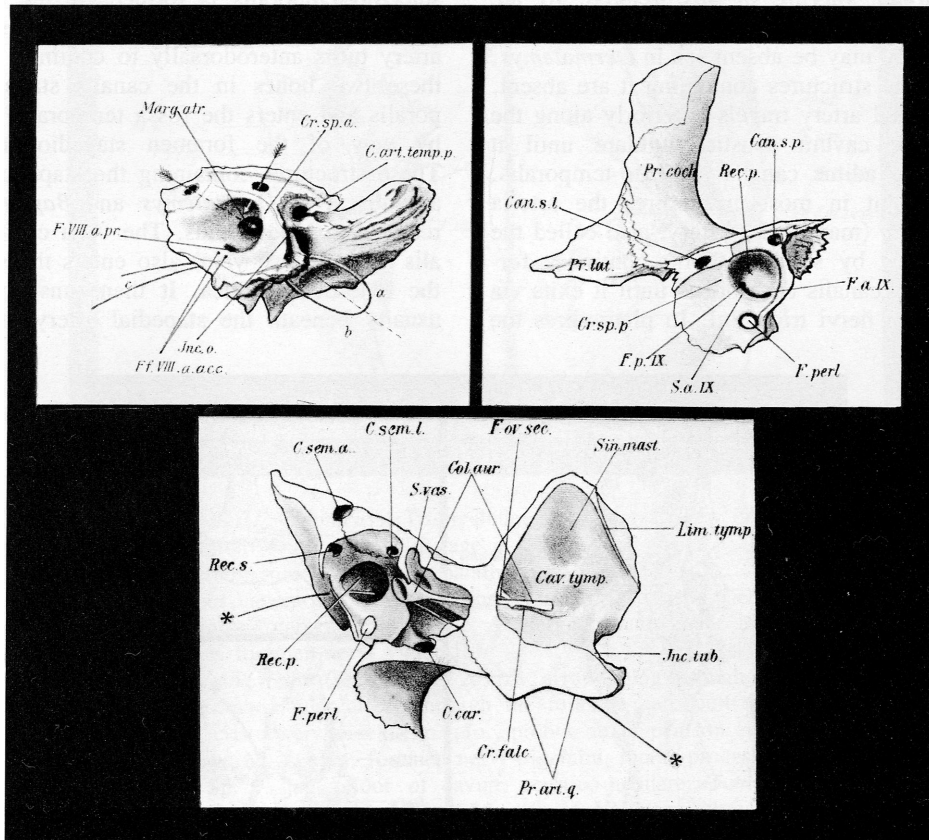


FIG. 105. *Trionyx sinensis* (*T. japonicus*), Trionychidae. Upper left, posterior view of right prootic (medial on left); upper right, anterior view of right opisthotic (medial on right). Lower, anterior view of a section through the supraoccipital, prootic, opisthotic, quadrate and pterygoid bones of the left side (see fig. 106 for position of section, medial is on left).

Abbreviations: a. b. c., lines going through the foramen nervi facialis; can. s. l., canalis semicircularis horizontalis; can. sp. p., canalis semicircularis posterior; c. art. temp. p., foramen stapedio-temporale; c. car., canalis caroticus internus; cav. tymp., cavum tympani; col. aur., columella auris; cr. falc., "crista falciformis" of Ogushi, 1911; c. sem. a., canalis semicircularis anterior; c. sem. l., canalis semicircularis horizontalis; cr. sp. a., "crista spiralis anterior" of Ogushi, 1911; cr. sp. p., "crista spiralis posterior" of Ogushi, 1911; f. a. IX., foramen internum nervi glossopharyngei; ff. VIII a. acc., foramen nervi acustici; f. ov. sec., incisura columellae auris; f. perl., fenestra perilymphatica; f. p. IX., foramen externum nervi glossopharyngei; f. VIII a. pr., foramen nervi acustici; Inc. o., foramen pro ramo nervi vidiani; Inc. tub., groove for eustachian tube; Lim. tymp., I don't know; marg. atr., recessus labyrinthicus prooticus; pr. art. q., articular surface of condylus mandibularis; pr. coch., processus paroccipitalis; pr. lat., processus paroccipitalis; rec. p., recessus labyrinthicus opisthoticus; rec. s., recessus labyrinthicus supraoccipitalis; s. a. IX., groove for glossopharyngeal nerve; sin. mast., antrum postoticum; s. vas., aditus stapediotemporalis; *——* path of glossopharyngeal nerve. After Ogushi, 1911.

prootic medially, the quadrate laterally and the pterygoid ventrally.

Anterior to the recessus scalae tympani the medial wall of the cavum acustico-jugulare consists of the ossifications surrounding the cavum labyrinthicum, that is, the prootic and opisthotic. The fenestra ovalis (see Cavum labyrinthicum) is the most prominent structure here and contains the basis columellae. The medial end of the stapes is surrounded by the paracapsular sinus (Baird, 1960, 1970) which also fills much of the cavum acustico-jugulare. The paracapsular sinus is a fluid-filled sac that probably "represents a specialized derivative of the medial part of a typical reptilian tympanic cavity rather than part of the periotic labyrinth" (Baird, 1970, p. 231). This structure is not found in any other reptiles and the unique nature of the cavum acustico-jugulare of turtles may be due at least in part to its role as a housing for the paracapsular sac.

The lateral wall of the cranioquadrate portion of the cavum acustico-jugulare is formed by the quadrate which contributes to the lateral half of the aditus canalis stapedio-temporalis, the canalis stapedio-temporalis, the foramen stapedio-temporale, and the canalis cavernosus. The extent of ossification of the incisura col-

umellae auris of the quadrate affects the degree of closure of the lateral wall of the cavum acustico-jugulare (see Quadrate).

The formation of the floor of the cranioquadrate portion of the cavum acustico-jugulare differs in degree and composition within turtles. The primitive condition, in which a floor is largely absent (as in most other reptiles), apparently can be seen in *Proganochelys*: "Posteriorly also the situation is primitive; the quadrate ramus of the pterygoid does not send any flange inward to floor the cranioquadrate passage as in all other known turtles [actually only in cryptodires], and the foramina for the vena capitis lateralis, the internal carotid, and the stapedia artery, as well as the fenestra ovalis, are all exposed in ventral view" (Parsons and Williams, 1961, p. 91). Collins (1970, figs. 13, 14) has presented an identification of structures in this area based on Parsons and Williams' work (*ibid.*). As Collins (*ibid.*) and Parsons and Williams (*ibid.*) have noted, the floor of the cavum acustico-jugulare in *Proganochelys* is more similar to primitive reptiles than to any known turtles. A comparison of this region among *Captorhinus*, *Proganochelys*, and *Casichelydia* (Gaffney, 1975d) should bring out important differences. In *Captorhinus* (see Romer, 1965, pp. 68-73; Fox and Bowman, 1966) the quadrate ramus of the pterygoid is a broad vertical plate extending posterolaterally from the region of the movable basiptyergoid articulation. What appears to be the homologue of the quadrate ramus in *Captorhinus* can be seen in all turtles, including *Proganochelys*. Although it is quite difficult to determine any sutures from the published accounts of Triassic turtles (Parsons and Williams, 1961; Jaekel, 1916), it appears that the quadrate ramus of the pterygoid in *Proganochelys* is essentially the same as in *Captorhinus*. The basiptyergoid articulation may be fused in *Proganochelys* and the primary neurocranial elements appear to contact the pterygoid above the cranioquadrate passage (cavum acustico-jugulare) in the Triassic turtle, but the pterygoid or neurocranial bones apparently do not take part in the floor of the cavum acustico-jugulare. In the *Casichelydia* the cranioquadrate portion of the

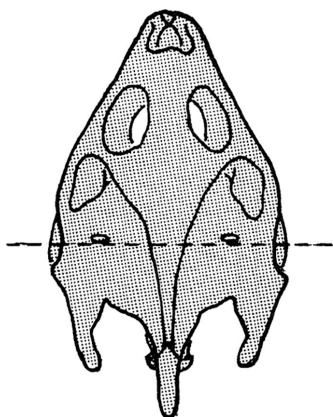


FIG. 106. Key for position of section in figure 105 (lower).

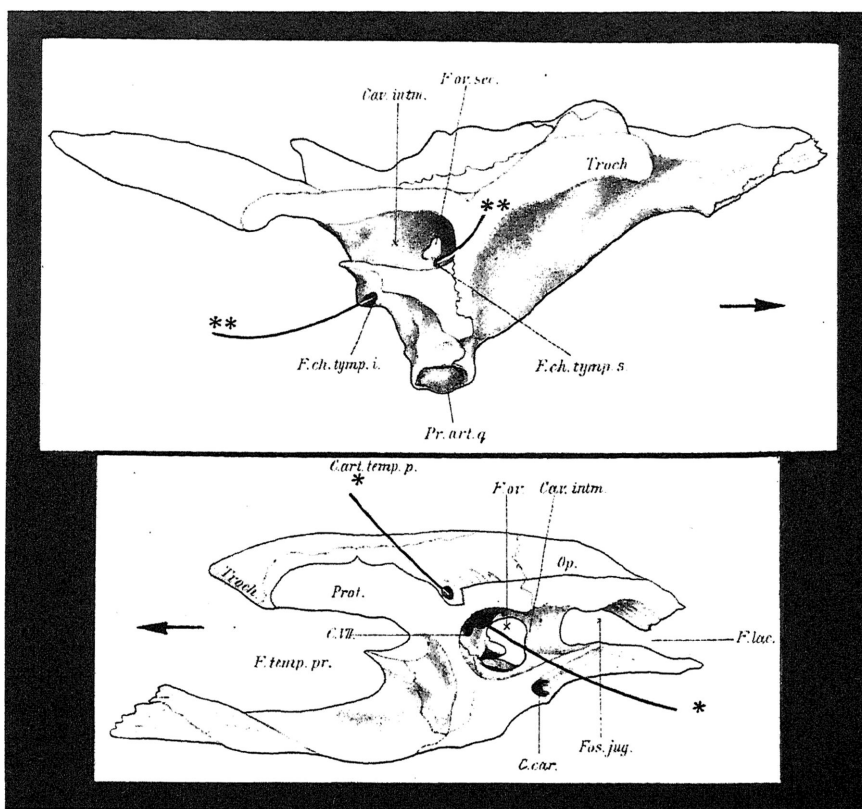


FIG. 107. *Trionyx sinensis* (*T. japonicus*), Trionychidae. This and the following two figures (108, 109) present a series of parasagittal sections through the left ear region. Figure 108 is a key to the sections and shows the skull cut into three pieces: a, the most lateral; b, the middle piece; and c, the most medial and remaining portion of skull. In figure 107, the upper one is a medial view of piece "a" (arrow shows anterior in all views), and the lower one is a lateral view of piece "b." In figure 109 the lower one is a medial view of piece "b" (which is thus seen from both sides) and the upper one is a lateral view of piece "c."

Abbreviations for figures 107 and 109: atr. amp. a., recessus labyrinthicus prooticus; C. art. temp. p., foramen stapedio-temporale; cav. intm., cavum acustico-jugulare; c. car., canalis caroticus internus; c. r. com. pal. VII., ventral opening of foramen pro ramo nervi vidiani; cr. oc., crista supraoccipitalis; cr. s., "crista superior" of Ogushi, 1911; cr. sp. a., "crista spiralis anterior" of Ogushi, 1911; cr. spr. p., "crista spiralis posterior" of Ogushi, 1911; c. sem. a., canalis semicircularis anterior; c. sem. l., canalis semicircularis horizontalis; c. sem. p., canalis semicircularis posterior; c. VII., foramen nervi facialis; f. a. IX., foramen internum nervi glossopharyngei; F. ch. tym. i., foramen chorda tympani inferius; F. ch. tym. s., foramen chorda tympani superius; ff. n. XII., foramen nervi hypoglossi; F. lac., fenestra postotica; f. jug. in., foramen jugulare anterius; f. l. c. car., foramen caroticum laterale; Fos. jug., cavum acustico-jugulare; f. ov., fenestra ovalis; fov. m., median depression on condylus occipitalis; F. ov. sec., incisura columellae auris; f. perl., fenestra perilymphatica; f. sph., foramen nervi trigemini; f. temp. pr., fossa temporalis inferior; f. VIII. a. acc., foramen nervi acustici; f. VIII. a. pr., foramen nervi acustici; inc. d. co., foramen aqueducti vestibuli; op., opisthotic; p. F. p. IX., foramen externum nervi glossopharyngei; Pr. art. q., articular surface of condylus mandibularis; pr. c. oc., condylus occipitalis; Prot., prootic; rec. p., recessus labyrinthicus opisthoticus; sa., pterygoid floor of recessus scalae tympani; semic. ant., canalis semicircularis anterior; semic. post., canalis semicircularis posterior; s. n. X. XI., medial limits of fenestra postotica (it would be the foramen jugulare posterius in a turtle with a bony separation between these structures); Troch., processus trochlearis oticum; X., hiatus acusticus; *———* canalis stapediotemporalis; **———** canalis chorda tympani quadrati. After Ogushi, 1911.

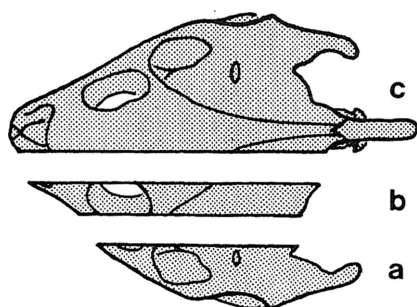


FIG. 108. See figure 107 for caption.

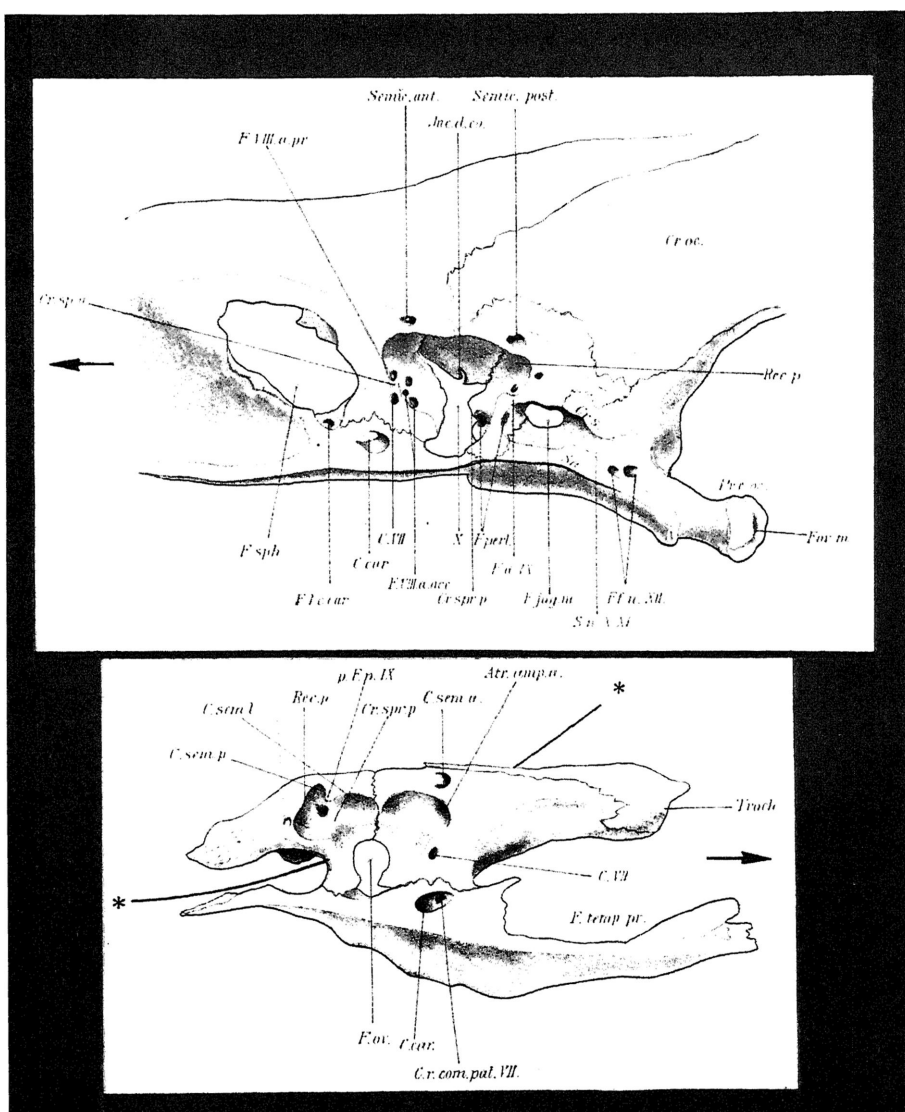


FIG. 109. See figure 107 for caption.

cavum acustico-jugulare is usually floored by a pterygoid flange (cryptodires) or by a portion of the prootic and/or quadrate (pleurodires). Most living pleurodires (with the notable exception of *Chelus* and most podocnemine pelomedusids) have only the anterior portion of the cavum acustico-jugulare floored and the Emydinae of McDowell often are characterized by the incomplete posterior extension of the pterygoid flange. However, even in these cases there is a significantly greater development of the bones involved than in *Proganochelys*.

There is a major difference between cryptodires and pleurodires in the composition of the floor of the cavum acustico-jugulare. In cryptodires the pterygoid forms a ventral brace between primary neurocranium and quadrate, whereas in pleurodires the quadrate and primary neurocranium make contact directly by means of processes lacking in cryptodires. Pleurodires have only the primitive quadrate ramus of the pterygoid which cryptodires have expanded posteromedially into a well-developed flange that not only floors the cavum acustico-jugulare but the cavum labyrinthicum also. In pleurodires the quadrate has a medial process, absent in cryptodires, that has a well-developed ventral contact with the prootic (highly modified but present in podocnemines) and the basisphenoid. The basisphenoid contact may be expanded, as in *Podocnemis*, or absent, as in *Chelus*, but the prootic contact is always present (it is thought to be hidden in ventral view in *Bothremys*, Gaffney and Zangerl, 1968, fig. 19D).

The soft structures traversing the cranioquadrate portion of the cavum acustico-jugulare also show differences between cryptodires and pleurodires. In all cryptodires the lateral head vein and the hyomandibular branch of the facial (VII) nerve run together in the canalis cavernosus, whereas in pleurodires the nerve is separated from the vein by bone and, therefore, lies outside the canalis cavernosus (see Prootic). The mandibular artery of pleurodires branches off the stapedial artery after the latter leaves the skull via the foramen stapedio-temporale. The mandibular artery of most cryptodires, however, exits from the foramen nervi tri-

gemini since it usually branches off the stapedial artery inside the cranioquadrate portion of the cavum acustico-jugulare rather than outside the skull as in pleurodires. Although the stapedial artery is reduced or absent in some cryptodires (trionychoids), and the mandibular artery comes off some other artery inside the skull (usually the palatine or internal carotid), it still exits via the foramen nervi trigemini. Most cryptodires, then, have the mandibular artery, hyomandibular nerve, and vena capitis lateralis in the canalis cavernosus, whereas pleurodires only have the lateral head vein in the canalis cavernosus (for extended discussion see Quadrate, Pterygoid, Prootic).

THE RECESSUS SCALAE TYMPANI PORTION OF THE CAVUM ACUSTICO-JUGULARE

The smaller portion of the cavum acustico-jugulare is termed the recessus scalae tympani and it is more intimately related to otic structures, as it contains the periotic sac as well as part of the paracapsular sinus (Baird, 1960, 1970). The recessus is usually formed from the following bones: basioccipital, opisthotic, exoccipital, pterygoid (in some cryptodires), and quadrate. The recessus scalae tympani is widely open laterally into the rest of the cavum acustico-jugulare. The processus interfenestralis of the opisthotic forms the anterior wall of the recessus and separates it from the cavum labyrinthicum. The fenestra perilymphatica penetrates the medial portion of the processus interfenestralis and allows the periotic sac to extend into the recessus scalae tympani from the cavum labyrinthicum.

Ventral to the fenestra perilymphatica is the hiatus postlagenum, another opening connecting the cavum labyrinthicum and the recessus scalae tympani. Dorsally, it is formed by the ventral edge of the processus interfenestralis of the opisthotic and ventrally by the basioccipital. The term hiatus postlagenum is modified from "postlagenar hiatus" of McDowell (1964). The hiatus is completely cartilaginous in many turtles and in some forms it seems to be absent. McDowell mentioned this opening (1964, p. 246) and stated that it is filled with connective

tissue in life and lies immediately posterior to the lagena. He also uses the size of the opening to help differentiate some Batagurinae from Emydinae: in *Clemmys* the hiatus postlagenum is "a small vertical slit," whereas in *Mauremys* and *Sacalia* (included in *Clemmys* by Wermuth and Mertens, 1961) it is "a large round hole, more than half as big as the perilymphatic foramen." Similarly, the hiatus is small in *Trionyx* but large in *Carettochelys*. McDowell also reported that the hiatus is present in all turtles except kinosternids and *Dermatemys*.

The anterior wall of the recessus scalae tympani also contains the foramen externum nervi glossopharyngei. The foramen usually occurs in the dorsolateral portion of the processus interfenestralis. Variation in the position of the foramen seems to be due primarily to the size of the processus interfenestralis (see Opisthotic).

The medial wall of the recessus scalae tympani is formed mostly by the basioccipital and exoccipital with variable contributions from the opisthotic. A prominent structure is the foramen jugulare anterius which transmits the vena cerebialis posterior (probably homologous with the vena jugularis of mammals), the vagus (X) and accessory (XI) nerves from the cavum cranii to the recessus scalae tympani (see Exoccipital and Opisthotic).

The posterior wall of the recessus scalae tympani is either cartilaginous or formed primarily by the exoccipital with smaller contributions from the opisthotic and basioccipital. The wall is usually pierced by the foramen jugulare posterius which transmits the vena cerebialis posterior, the vagus (X) nerve, and the accessory (XI) nerve from the recessus scalae tympani to the outside of the skull. Some forms,

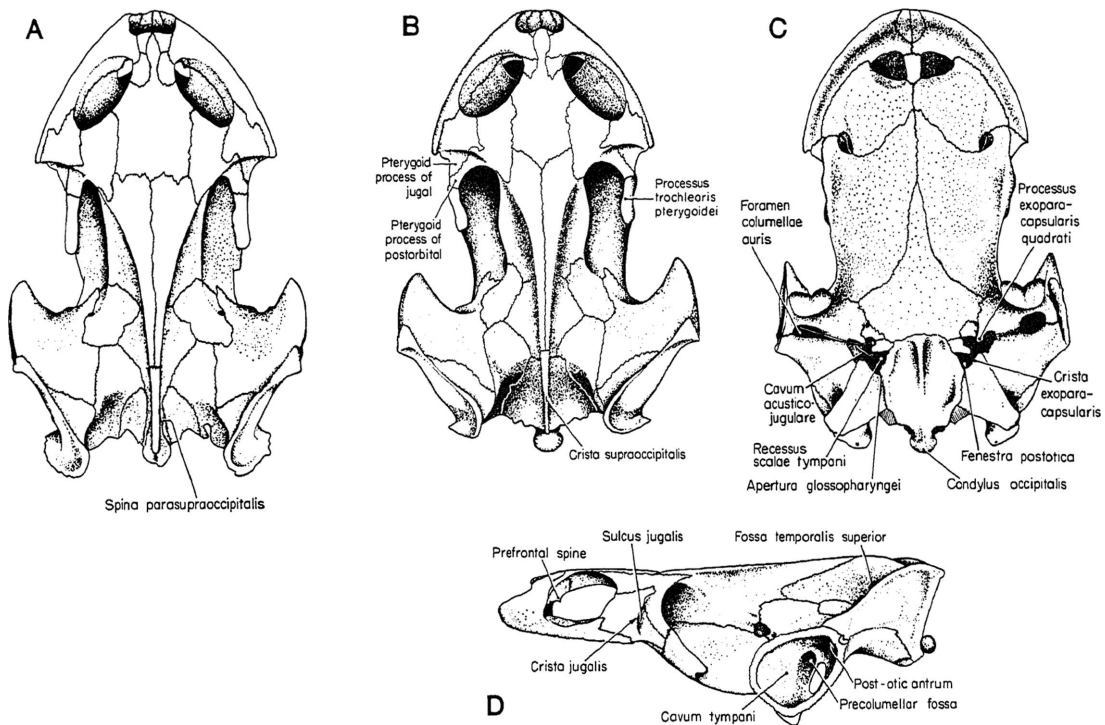


FIG. 110. *Chelodina*, Chelidae. Views of skulls showing features useful in describing chelid skulls. Chelids are particularly unusual in the morphology of the postorbital region. A. *Chelodina parkeri* (AMS 21434); B, C, D. *Chelodina siebenrocki* (AMS 40696). After Rhodin and Mittermeier (1976).

such as the cheloniids, lack a bony separation between the foramen jugulare posterior and the more lateral fenestra postotica (see below). The foramen jugulare posterius is formed by the exoccipital dorsally, medially, and ventrally. In most turtles a small process of the opisthotic completes the lateral border of the foramen jugulare posterius and separates the foramen from the fenestra postotica. In some turtles this contribution from the opisthotic can become enlarged and form as much as half of the border of the foramen jugulare posterius.

The floor of the recessus scalae tympani is usually formed by one or more of the following bones: pterygoid (as in cheloniids), exoccipital (most cryptodires), and basioccipital (most turtles). In some pleurodires (e.g., *Pelusios* and *Emydura*) much of the floor is cartilaginous and opens ventrally in the bony skull. Most members of the Emydinae of McDowell (1964, p. 214) lack the posterior extension of the pterygoid found in most cryptodires. This extension floors part of the recessus scalae tympani and cavum labyrinthicum and when it is reduced nearly all of the foot of the processus interfenestralis is exposed in ventral view.

THE FENESTRA POSTOTICA

The fenestra postotica is the posterior opening of the cavum acustico-jugulare and is quite variable among turtles in the degree to which it is subdivided and limited by bone. A number of structures pass through this region, the most prominent being: the arteria stapediale, the vena capitis lateralis, the vena cerebialis posterior, the hyomandibular branch of the facial (VII) nerve, the glossopharyngeal (IX) nerve, the vagus (X) nerve, and the accessory (XI) nerve. Commonly the vena cerebialis posterior is separated off in the foramen jugulare posterius. In life, cartilage fills most of the fenestra postotica so that even the most "open" skulls have a functionally enclosed cavum acustico-jugulare.

Proganochelys lacks a ventral limit for the cavum acustico-jugulare and differs from the Casichelydia in having a very poorly defined

fenestra postotica. The baenoids and chelonoids lack a bar between the foramen jugulare posterius and the fenestra postotica. Both of these groups also may have an open incisura columellae auris and, therefore, a fenestra postotica that lacks well-defined bony medial and lateral limits.

Most turtles have a bony bar (usually formed by the opisthotic and/or exoccipital) between the fenestra postotica and the foramen jugulare posterius. Such groups as chelydrids, most emydids, *Dermatemys*, and kinosternids have this bar but no bony subdivisions of the fenestra postotica. In some emydids, such as *Deirochelys*, the glossopharyngeal (IX) nerve is enclosed by bone and excluded from the fenestra. Testudinids, some trionychids, and *Carettochelys*, on the other hand, have greatly reduced the size of the opening apparently by ossifying the cartilage already present. In these forms the glossopharyngeal (IX) nerve has a separate opening (in *Cyclanorbis* this is on the medial side of the bony bar between the fenestra postotica and foramen jugulare) and the lateral head vein and stapediale artery run through what remains of a much reduced fenestra postotica. In some trionychids (*Cycloderma*, for example) the fenestra is in the form of a horizontal figure 8 with the stapediale artery in the lateral portion and the lateral head vein in the medial portion.

Trionychids have a characteristic occipital morphology in which a horizontal shelf is developed beneath the foramina nervi hypoglossi and the foramen jugulare posterius. This shelf is usually continuous posteriorly with the tuberculum basioccipitale and may extend dorsolaterally between the fenestra postotica and the foramen jugulare posterius. Within the genus *Trionyx* the bar between the fenestra postotica and the foramen jugulare posterius may be absent (most specimens of *T. ferox*; some specimens of *T. triunguis*, Loveridge and Williams, 1957, fig. 53; and *T. sinensis*, Ogushi, 1911, fig. 17), it may be reduced but formed by the opisthotic (some specimens of *T. ferox*), or it may be formed by ascending processes of the pterygoid (some specimens of *T.*

triunguis, Loveridge and Williams, 1957, fig. 54). In *Pelochelys* the fenestra postotica and foramen jugulare posterius are completely continuous. The ventral shelf seen in other trionychids is quite extensive in *Pelochelys* and is

paralleled by a dorsal shelf above the fenestra. The lateral region of the fenestra postotica in *Pelochelys* has a foramen that probably contains either the arteria stapediales or the vena capitis lateralis.

LOWER JAW ELEMENTS

DENTARY

Figures 111, 112

CONTACTS: The dentary meets the other jaw elements posteriorly in a complex series of squamous and interleaving sutures. In most turtles the contacts are as follows: coronoid posterodorsally, surangular posterolaterally, angular posteroventrally, and prearticular posteromedially. A splenial contact may be present medially (as in chelids and some cryptodires; see Splenial) and in *Dermochelys* the dentary contacts only the surangular and angular.

STRUCTURES: The dentary is the dominant bone in the lower jaw and bears nearly all of the triturating surface. In all turtles, except the chelids *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa* (see Gaffney, 1977a), both rami are fused at the symphysis. The absence of fusion in these chelids I consider a derived feature; also *Hesperotestudo* (Bramble, 1971) is reported to have a symphyseal suture, which is presumably derived for this form as well. The dentary usually extends more posteriorly on the lateral surface with most of the other mandibular elements on the medial surface.

The triturating surfaces of the lower jaw can be described in much the same terms as the upper jaw (see Maxilla). A lateral labial ridge forms the outer margin of the surface and a medial lingual ridge may be found along the inner edge. At the symphysis a pointed dorsal projection or hook may be formed, as in *Macrolemys* and *Erymnochelys*. The posterior limits of the rhamphotheca on the triturating surface is often marked by a short dorsal process or spur that also usually marks the anterior-

most attachment of the adductor jaw musculature.

Variation in the lower jaw triturating surface morphology is comparable in magnitude and type to that seen in the upper jaw triturating surface. Some forms (e.g., *Chelus*, *Glyptops*, and *Dermochelys*) have only the labial ridge developed with a sharply sloping (or nonexistent) triturating surface and no lingual ridge. Most turtles, however, have a triturating surface that is about as wide as each ramus and has a low lingual ridge. Although the lingual ridge is usually lower than the labial ridge, it may be the same height as the labial ridge (e.g., *Geochelone*, *sensu* Loveridge and Williams, 1957) or it may be higher than the labial ridge (e.g., *Podocnemis expansa*). The triturating surface is usually flat or sloping medially but various structures may be present. The surface may be a simple trough (e.g., *Geochelone*) or a parallel ridge (or ridges) may separate a series of troughs (e.g., *Batagur baska*). *Dermatemys* has a ridge running at right angles to the jaw ramus near the symphysis and it separates off a roughly triangular area around the symphysis that is lower than the areas posterior to the ridge. In most turtles the lower structures fit into complementary structures on the upper triturating surfaces but this is not always the case. One of the most extreme examples of this is *Bothremys* (Cretaceous) in which the lower jaw has a pair of large pits that open anterodorsally and extend posteriorly as conical cavities well beneath the coronoid processes. When the lower jaws are shut a spherical cavity on each side is the result (Gaffney and Zangerl, 1968). Forms with sec-

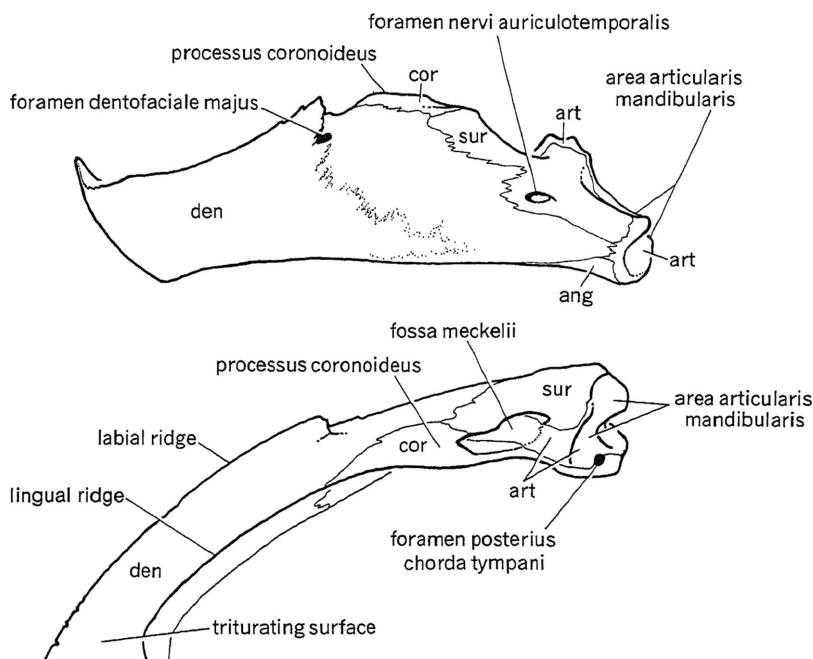


FIG. 111. Lower jaw of *Chelydra serpentina* (AMNH 67015), Chelydridae; Bronxville, Westchester County, New York. Upper, lateral view of left ramus; lower, dorsal view of right ramus. From Gaffney (1972b).

ondary palates usually have expanded mandibular triturating surfaces. Zangerl (1953, fig. 61) described a structural series of toxochelyids that shows an increase in triturating surface area. As is the case with the upper triturating surfaces, *Erquelinnesia* (Eocene) has the most extensive mandibular triturating surface described. Zangerl (1971) compared the osteopygine *Erquelinnesia* and other chelonioids with secondary palates by means of a line connecting the foramen dentofaciale majus of each ramus. His results show a considerable increase in area along the symphysis. *Stereogenys*, a podocnemine pleurodire, with an incipient secondary palate also has a broadly expanded lower triturating surface that is similar to the osteopygines.

The medial surface of the dentary has a longitudinal depression, the sulcus cartilaginis meckelii, which contains the remnant of Meckel's cartilage (Kunkel, 1912). Posteriorly, the sulcus is continuous with the fossa

meckelii, but the latter is only partly formed by the dentary. The sulcus cartilaginis meckelii of *Chelus* disappears just anterior to the foramen intermandibularis medius. The foramen alveolare inferius also occurs on the medial face of the dentary, usually in the posterior portion of the sulcus cartilaginis meckelii. This foramen leads anteriorly into the canalis alveolaris inferior. According to Soliman (1964, figs. 11-13), the canalis contains the ramus alveolaris inferior and ramus cutaneous externus which are both branches of the mandibular (V_3) nerve, and small unnamed blood vessels. The canalis may continue across the symphysis as in *Chelonia* or it may end before the symphysis as in *Chelydra*. The foramen dentofaciale majus is an opening on the lateral surface of the dentary, usually found ventral to the dorsal spur mentioned above that marks the posterior limits of the rhamphotheca. The foramen leads into a short canal that extends anteroventromedially into the canalis alveolaris inferior.

Because information in the literature on the arterial contents of these structures is limited, Dr. Philip Albrecht has kindly supplied me with the results of his observations on lower jaw arteries. He examined this region in *Chrysemys* and *Pelomedusa* and made the following generalizations: the mandibular artery enters the fossa meckelii and splits into two branches. One branch exits from the foramen intermandibularis medius to supply tissue medial to the triturating surface. The other artery goes through the foramen alveolare inferius and enters the canalis alveolaris inferior. No artery

appears to be present in the foramen dentofaciale majus.

The extent of the horny rhamphotheca on the outer surface of the dentary can usually be seen in the bony skull by the distribution of many small foramina, presumably serving as nutrient canals for the rhamphotheca. In forms with thin and less extensive rhamphotheca (such as chelids) the foramina are small and sparse while in forms with extensive and thick rhamphotheca (such as cheloniids) the foramina are larger and more numerous.

The lateral surface of the lower jaw also is

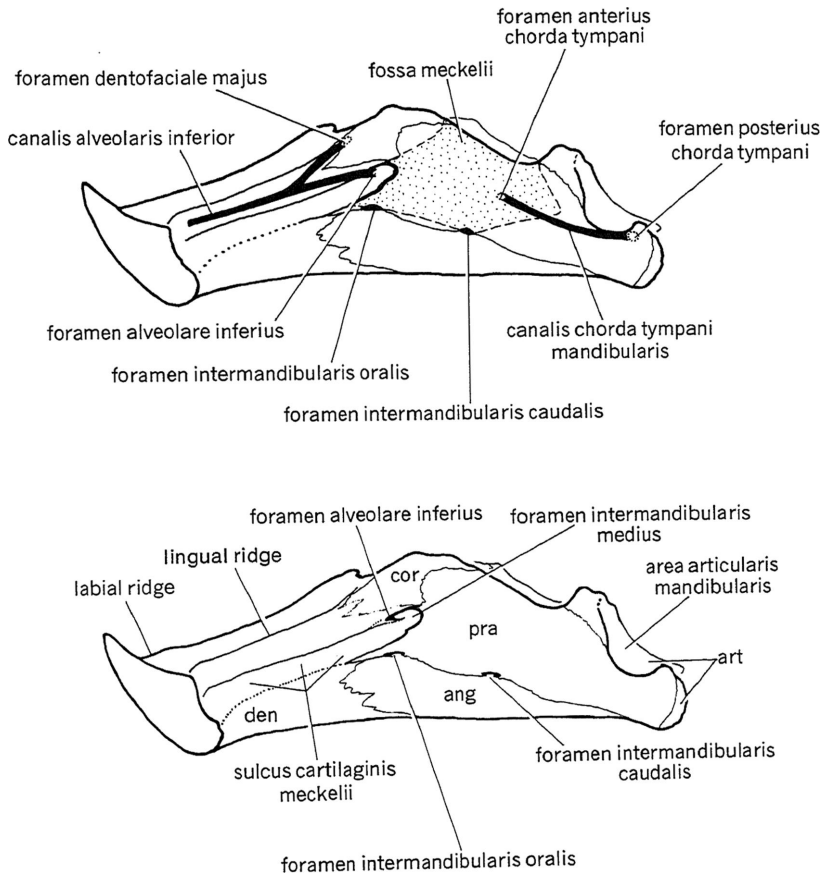


FIG. 112. Medial views of right lower jaw ramus of *Chelydra serpentina* (AMNH 67015), Chelydridae, Bronxville, Westchester County, New York. Upper, internal details shown, extent of fossa meckelii stippled, internal canals black, hidden foramina open circles, visible foramina, solid. Lower, external structures of medial surface. From Gaffney (1972b).

the attachment area for the M. adductor mandibulae externus pars superficialis (Schumacher, 1954, 1955a, 1955b, 1973). A depression or concavity is variably developed in this area which is ventral to the processus coronoideus and between the posterior limits of the rhamphotheca and the jaw articulation. The dentary, coronoid, and surangular usually make up this depression but some of the bones may be excluded from it as is the dentary in *Podocnemis expansa*. Due to the extreme reduction of the posterior section of the jaw, *Dermochelys* lacks this depression and it is also absent in *Chelus*, although the jaw is not reduced.

ANGULAR

Figures 111, 112

CONTACTS: The usual contacts of the angular are as follows: dentary anteriorly, splenial (when present) and prearticular dorsally on the medial side, and articular posteriorly. The surangular may contact the angular posteriorly on the lateral jaw surface if the dentary does not send a process back to reach the articular. It should be emphasized again that the bones in the posterior part of the mandible overlap and interdigitate and the internal contacts may be different and more complex than the external ones.

STRUCTURES: The angular is usually a long and slender sheet that curves around the posterior half of the mandible from the anteromedial surface to the posterolateral surface and forms much of the posteroventral surface of the jaw. In many forms the anteromedial portion reaches the sulcus cartilaginous meckelii (e.g., trionychids) or it may be separated by the splenial or prearticular.

The angular usually forms the ventral margin of the foramen intermandibularis caudalis, two openings into the fossa meckelii that lie on the medial surface of the mandible usually between the angular and prearticular (see Prearticular for discussion). The foramen intermandibularis oralis is often only a notch or is completely confluent with the foramen intermandibularis medius.

SURANGULAR

Figures 111, 112

CONTACTS: The surangular is a sheetlike element that lies behind and somewhat dorsal to the dentary. A posteroventral process of the dentary may cover more or less of the lateral surface of the surangular. The other contacts are usually as follows: the coronoid anterodorsally, the angular posteroventrally, and the articular medially. The angular-surangular contact may be lacking if the dentary reaches all the way to the articular. In many trionychids the prearticular and surangular meet either at the posterior edge of the fossa meckelii in front of the articular or they subdivide the fossa meckelii by meeting in its center (e.g., *Cycloderma frenatum*). In *Dermochelys* the surangular only meets the dentary and angular due to the absence of the coronoid and the unossified condition of the articular.

STRUCTURES: The surangular is a roughly platelike bone forming much of the lateral wall of the fossa meckelii. The fossa meckelii is the space behind the processus coronoideus and anterior to the jaw articulation. It is open dorsally and communicates anteriorly with the sulcus cartilaginous meckelii. The upper opening of the fossa is usually formed by the coronoid anteriorly, the surangular laterally, the articular posteriorly and the prearticular medially. The opening may be relatively large, as in cheloniids, or it may be more constricted as in trionychids. In fact, some trionychids (e.g., *Cycloderma frenatum*) may restrict the opening to two foramina for the nerves and blood vessels. Schumacher (1954, 1955a, 1955b, 1973) reported that muscle fibers of the M. pseudotemporalis and M. adductor mandibulae posterior may extend through the upper opening and insert in the fossa. In addition the mandibular (V_3) branch of the trigeminal nerve and the mandibular artery enter the lower jaw via this opening (Fuchs, 1931; Poglayen-Neuwall, 1953; McDowell, 1961; Soliman, 1964; Albrecht, 1967; Schumacher, *ibid.*).

The foramen nervi auriculotemporalis usually penetrates the surangular (although apparently this is not invariable) and allows

communication between the lateral surface of the jaw and the fossa meckelii. The foramen (or in some cases foramina, e.g., *Podocnemis expansa*) contains the auriculotemporalis nerve of Fuchs (1931) which appears to be the ramus cutaneous recurrens branch of the mandibular (V_3) nerve of Soliman (1964, fig. 15). In some cryptodires (e.g., *Staurotypus*, *Terrapene*) there is another foramen (here unnamed) in the surangular that communicates with the foramen nervi auriculotemporalis and the fossa meckelii.

The posteromedial part of the surangular may bear part of the area articularis mandibularis as in Recent cheloniids and trionychids.

CORONOID

Figures 111, 112

CONTACTS: The coronoid usually contacts the dentary anteriorly and laterally, the surangular posterolaterally, the prearticular posteroventromedially and (when present) the splenial ventromedially. The coronoid is absent in *Dermochelys*. The prearticular contact is reduced or absent in chelids and its contact area is occupied by the splenial.

STRUCTURES: The coronoid is a roughly triangular bone lying about midway along each ramus on the dorsal side of the jaw. Its apex is the processus coronoideus, posteriorly the coronoid borders the fossa meckelii, and anteriorly it reaches the posterior border of the triturating surface. The processus coronoideus is a dorsally directed process formed primarily by the coronoid, although in some forms the dentary and surangular may be dominant constituents (e.g., *Chelus*). Fibers of the M. adductor mandibulae externus, but most importantly, the main external adductor tendon (boden-aponeurosis) attach on the coronoid process (Schumacher, 1954, 1955a, 1955b, 1973). The processus may be quite high and well developed (e.g., trionychids) or it may be lower than the dorsal portion of the dentary (e.g., *Podocnemis expansa*). The coronoid may extend anteriorly onto the triturating surface and be covered by rhamphotheca (e.g., *Podocnemis expansa*, *Staurotypus*) or it may not extend anteriorly (e.g., *Chelus*).

ARTICULAR

Figures 111, 112

CONTACTS: The articular contacts the surangular laterally, the angular ventrally, and prearticular medially. In some forms (e.g., *Chelydra*) the long process of the dentary reaches the lateral surface of the articular. The articular does not ossify in *Dermochelys* but remains cartilaginous.

STRUCTURES: The articular is an irregular blocklike bone lying at the posterior end of the jaw. It is the only lower jaw element that ossifies from cartilage and it ossifies in the posterior end of Meckel's cartilage. The dorsal portion of the articular bears most of the area articularis mandibularis, the surface that articulates with the condylus mandibularis of the quadrate. In some cases the surangular and/or prearticular may also participate in forming the area articularis mandibularis. The posterior limits of the fossa meckelii are usually formed by the articular (exceptions include some trionychids). The form of the area articularis mandibularis has been used in many classifications as a method of distinguishing between cryptodires and pleurodires. In pleurodires the articular has the form of a hemisphere, whereas in cryptodires the surface usually has a median longitudinal ridge separating two concavities. Posterior to the area articularis mandibularis is an attachment area for the M. depressor mandibulae. Usually a convexity on the most posterior part of the jaw is the main attachment site but a retroarticular process may be developed, as in trionychids.

The articular usually forms all or part of the foramen posterius chorda tympani, which can usually be found medial to the area articularis mandibularis between the articular and prearticular (see Prearticular for discussion) or posterior to the area articularis mandibularis but within the articular.

PREARTICULAR

Figures 111, 112

CONTACTS: The usual contacts of the prearticular are as follows: coronoid antero-

dorsomedially, articular posteromedially, and angular ventrally. In some forms there may be a short anterior contact with the dentary (e.g., *Chelydra*), and when the splenial is present it is sutured to the anterior edge of the prearticular. In *Dermochelys* the prearticular contacts none of the other bones because it is attached to the medial side of the unossified articular cartilage.

STRUCTURES: The prearticular is a large flat sheet covering much of the posteromedial surface of the lower jaw and forming most of the medial wall of the fossa meckelii. The anterior edge of the prearticular usually forms the medial half of the foramen intermandibularis medius, the large anterior opening of the fossa meckelii into the sulcus cartilaginis meckelii. The ramus intermandibularis medius of the mandibular (V_3) nerve and usually (as in *Chelydra*) the remnants of the meckelian cartilage pass through the foramen intermandibularis medius. Two foramina occur along the ventral edge of the prearticular, usually within the angular-prearticular suture. Both allow communication between the medial surface of the jaw and the fossa meckelii. The anterior one is the foramen intermandibularis oralis and contains the ramus intermandibularis oralis of the mandibular (V_3) nerve. The foramen may also be present as a notch or indentation in either angular or prearticular, or it may be completely absent. The more posterior opening is the foramen intermandibularis caudalis which contains the ramus intermandibularis caudalis of the mandibular (V_3) nerve.

The chorda tympani nerve enters the lower jaw in the region just medial to the area articularis mandibularis either in the suture formed between the articular and prearticular or within the articular. This opening is the foramen posterius chorda tympani and it can usually be seen on the medial edge of the area articularis mandibularis. The foramen opens into an anteriorly directed canal, the canalis chorda tympani mandibularis. The anterior opening of the canalis is the foramen anterius chorda tympani and enters the fossa meckelii where it is usually not visible superficially. The prearticular and/or

articular usually forms most of these structures. Fuchs (1931, p. 266) reported individual variation in *Podocnemis expansa* in which the following conditions may occur: the nerve is external to the bone, the nerve enters the prearticular but exits medially and does not enter the fossa meckelii, the nerve enters the prearticular and exits in the normal manner into the fossa meckelii, and the nerve passes between the prearticular and articular but does not form a canal within the prearticular. Fuchs (1931) also indicated another canal in *Podocnemis expansa*, the apertura medialis canalis transversi, which goes through the jaw to the lateral surface. Soliman (1964, p. 255) indicated the absence of the chorda tympani in *Eretmochelys* and *Chelonia* (see Quadrate) but I was unable to locate the canalis chorda tympani mandibularis or its associated foramina in any of the living cheloniids. Poglayen-Neuwall (1953) reported the chorda tympani in *Caretta*.

SPLENIAL

Figures 161, 273

CONTACTS: The splenial is usually bounded anterodorsally by the coronoid, posterodorsally by the prearticular, posteroventrally by the angular, and anteroventrally by the dentary.

The splenial is absent in most Recent turtles but it occurs commonly in Mesozoic forms (Parsons and Williams, 1961; Gaffney, 1975b, 1975c). Chelids have a well-developed splenial and Romer (1956, p. 505) reported one in *Platysternon* and emydines. In one (AMNH 30115) of three specimens of *Platysternon megacephalum* I found a possible splenial in the right ramus but not the left. Siebenrock (1897) reported a splinter-like splenial in *Chrysemys ornata*.

STRUCTURES: The splenial is a flat trapezoidal bone that occupies the area anterior to the prearticular on the medial surface of the jaw. The anterior edge of the splenial forms part of the foramen intermandibularis medius and a portion of the lateral wall of the fossa meckelii.

A REVIEW OF PREVIOUS WORK ON TURTLE SKULL MORPHOLOGY WITH LITERATURE REFERENCES TO TURTLE SKULL FIGURES AND WORKS OF SYSTEMATIC INTEREST

This section has two purposes: (a) to review the turtle skull literature and (b) to present the classification I follow here. The main body of the text is a family by family compilation of references to turtle skull figures that I have found useful. It is not intended to be thorough in the sense of including every known figure but rather to list those figures that might be important when dealing with a particular group. Some taxa, such as *Dermochelys*, are relatively well-figured and I have listed the best figures and ignored the others; such taxa as the Chelidae, however, are poorly known and I mention nearly all the figures I could find, even poor ones. In general, the older works mentioned are limited to the latter part of the nineteenth century, because even though such monographs as Cuvier (1824) and Wagler (1830) contain high quality turtle skull figures, they are probably not easily accessible to most readers of this chapter. In general, poor or grossly incorrect figures are not listed¹ but a few are mentioned because they have been referred to in the literature. Gross errors are corrected but in general I have taken no notice of inaccuracies in published figures not appearing in this chapter. Previously published figures that I repeat in this chapter are indicated by an asterisk (*) in the following reference list. I have tried to update the nomenclature but have made little effort to substantiate the original identification in most cases.

Important references for the systematics of particular groups are noted under the family headings below, but I would like to mention some more general works first. Kuhn (1964)

and Mlynarski (1976) for fossils and Wermuth and Mertens (1961, 1977) for Recent species are the primary sources for literature references of turtle genera and species. Although Romer (1956) is out of date, it is still useful as an introduction to the traditional classification of turtles (as well as having higher category diagnoses), whereas the *Traité de Paléontologie* contribution by Bergounioux (1955) deserves the ignorance it has received. Sukhanov (1964) seems to be more extensive than other fossil turtle reviews but not having read it, I cannot judge its quality. Both Pritchard (1967) and Mlynarski (1969) are good semipopular illustrated reviews of living and fossil turtles, respectively.

The higher category classification used here reflects a phylogenetic hypothesis based on shared derived characters and is consistent with the ideas known as phylogenetic systematics, or cladism. I have discussed this phylogeny and its ideologic basis elsewhere (1975d) and the reader should see that paper for further information and references. At the present time I cannot present a classification down to generic levels of Recent and fossil turtles that is completely consistent with phylogenetic systematics simply because I have not developed the requisite phylogenetic hypotheses. Furthermore, I do not think that this is the place to announce systematic novelties. Therefore, I have combined various works, including my own, into a classification that uses my hypotheses where published but relies on other authors in areas that I have not worked.

A distinct difference between this classification and others of Recent and fossil turtles (such as Romer, 1956; Zangerl, 1969) is the absence of taxa that I consider at the present time undiagnosable using cranial characters. This removes a host of fossil forms either lack-

¹Some high quality figures may not be listed because I either am not aware of them or I forgot to include them. I hope the authors of such figures will not think that I have omitted them because they are unsatisfactory.

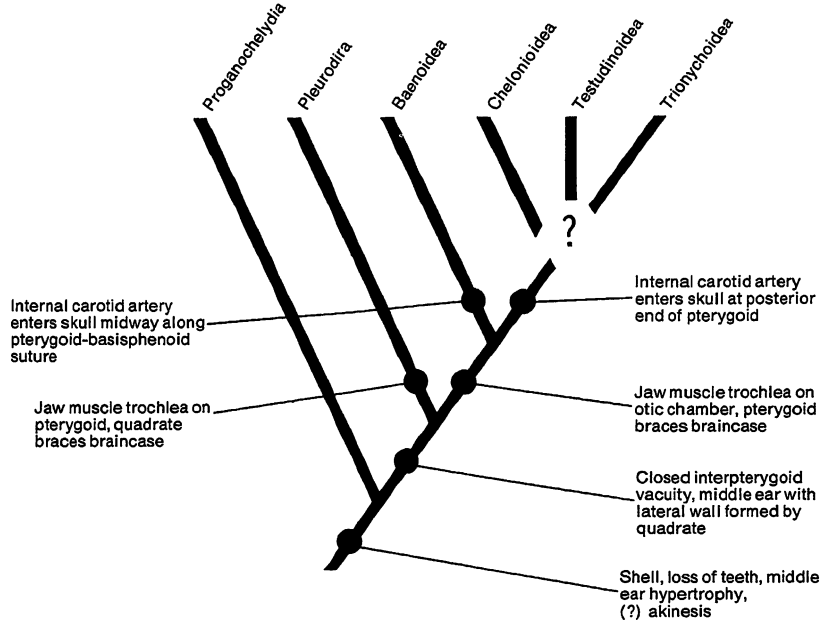


FIG. 113. A theory of relationships among the higher categories of turtles. This cladogram indicates the relative position of common ancestors and a few shared derived characters diagnostic of particular lineages. Other morphologic and temporal parameters are not expressed. See Gaffney (1975d) for discussion of phylogeny and classification.

ing skulls or with unprepared or poorly preserved skulls (as well as those forms that for one reason or another I have not had an opportunity to examine).

The triumvirate of chelonian craniology is Siebenrock (1897), Ogushi (1911), and Nick (1912). Siebenrock wrote the only attempt to compare Recent turtle skulls in detail and this work is by far the most important single reference on turtle skull morphology.¹ Ogushi (1911) produced one of the most intensive and well-illustrated studies of the skull in a single species (*Trionyx sinensis*). Unfortunately, the text is not comparative and is, therefore, less useful than Siebenrock for systematic work. A later (1913) paper by Ogushi described the soft anat-

omy of the skull and supplies information on the contents of bony structures. Nick's (1912) paper is also somewhat comparative but restricted mostly to *Chelydra*, cheloniids, and with particular emphasis on *Dermochelys*. The sections in color of these turtles are extremely useful.

Other works of general interest are listed below in chronological sequence: Bojanus (1819) has a series of cranial figures showing bony structures and soft parts. Some of the figures are natural size and are too small and the labels are outdated, but the recent reprinting of this work and its overall high quality balance the disadvantages. Kesteven (1910) is the only detailed description of a Recent turtle skull in English. The description is not comparative, soft structures are not described in detail, and the figures are somewhat lacking in aesthetic polish. Nonetheless, the figures are particularly useful because it is one of the few papers that illustrates different views of the same bone.

¹The genera *Dermochelys*, *Dermatemys*, *Carettochelys*, and *Platysternon* have various unique features among the living turtles. Unfortunately, specimens of these forms were not available to Siebenrock and some of his statements about them are based on earlier authors' errors.

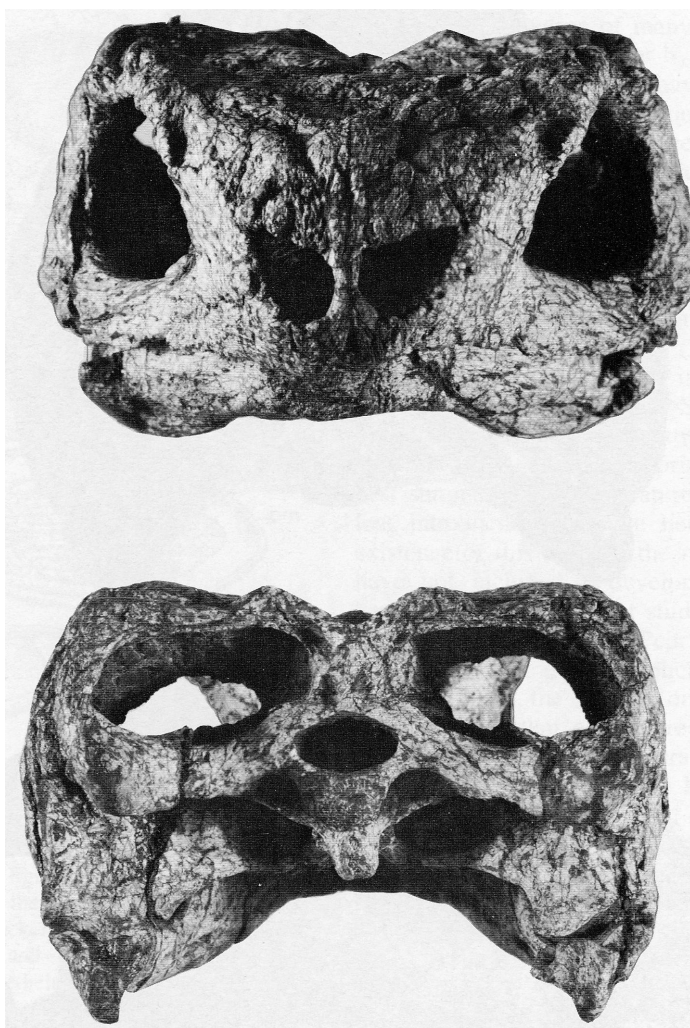


FIG. 114. *Proganochelys quenstedti* (Staatliches Museum für Naturkunde, Stuttgart), Proganochelyidae, Late Triassic, Germany. Upper, anterior view; lower, posterior view. From Parsons and Williams (1961). I am indebted to Drs. Parsons and Williams for sending me the original figures for this and figure 115.

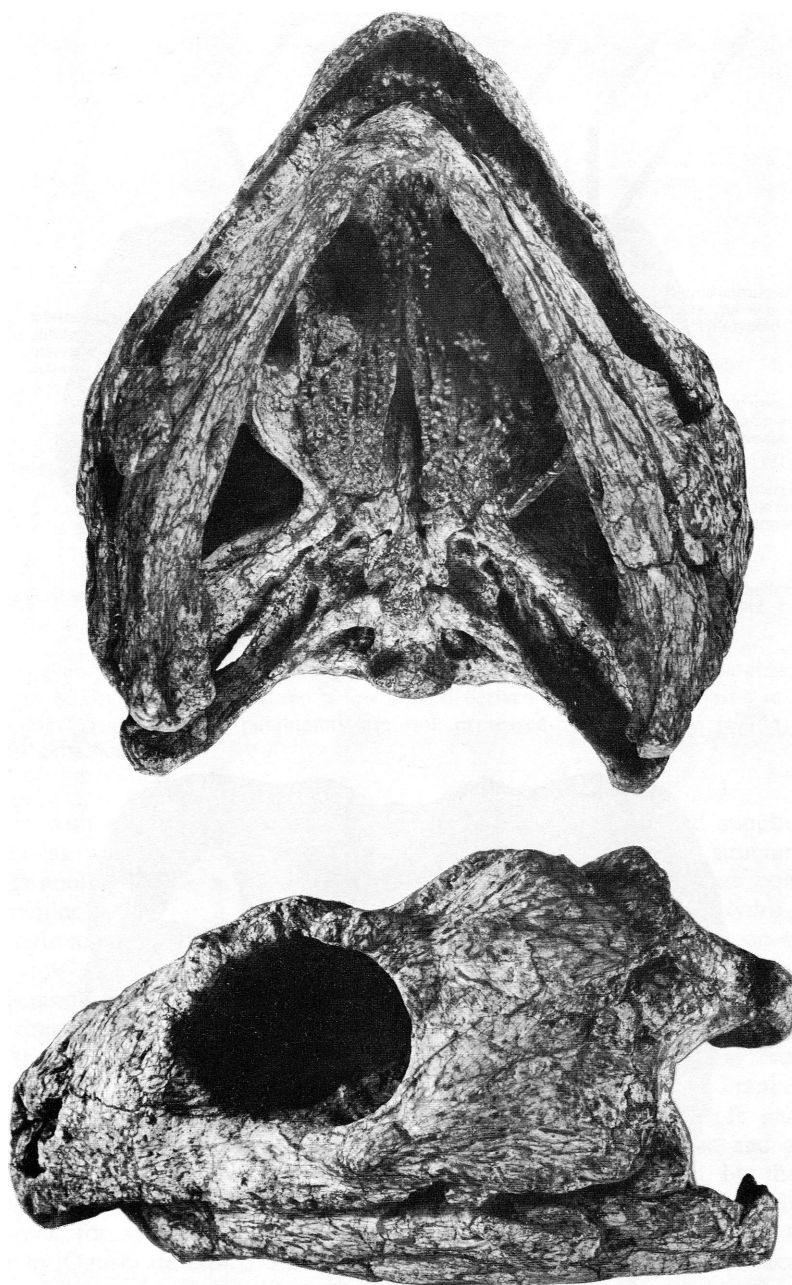


FIG. 115. *Proganochelys quenstedtii* (Staatliches Museum für Naturkunde, Stuttgart), Proganochelyidae, Late Triassic, Germany. Upper, palatal view; lower, left lateral view. From Parsons and Williams (1961).

Romer (1956) is still the best introduction to turtle skull morphology although it is somewhat out of date. Wegner (1959) presents an excellently illustrated account of *Dermochelys* skull

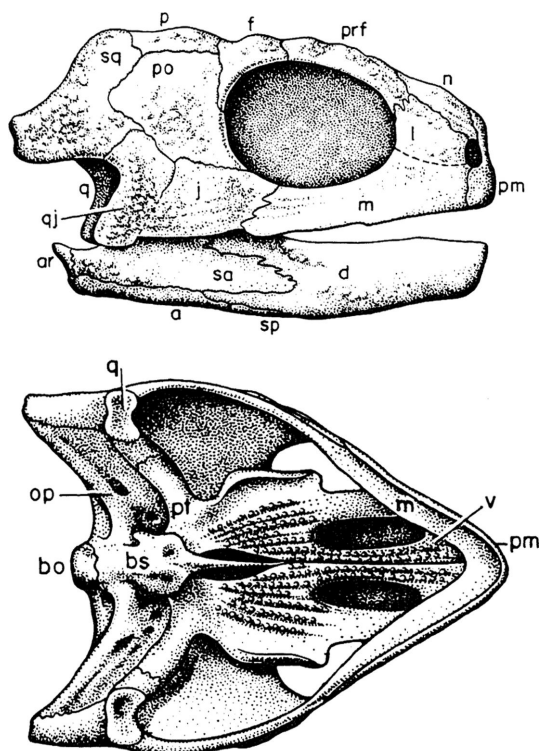


FIG. 116. *Proganochelys quenstedti*, Proganochelyidae, Late Triassic, Germany. Upper, right lateral view; lower, palatal view. Reconstruction from Romer (1966) [with permission from Univ. Chicago Press]. These figures are based on Jaekel's (1916) illustrations of the Berlin specimen (called *Triassochelys dux* by Jaekel) with considerable modification using Parsons and Williams' figures of the Stuttgart material. Nonetheless, these figures should be considered speculative as sutures are not readily discernible in Parsons and Williams' figures and the Berlin specimen is somewhat crushed. Furthermore, the restoration indicates an open foramen palatinum posterius, whereas the known photographs of this region (figs. 115 and 117) do not suggest a morphology very different from *Chelydra* in this region. See Gaffney (1975d, p. 424) for further discussion.

morphology. Parsons and Williams (1961) is an important study of fossil cryptodire skulls from the Jurassic that fills a considerable gap. Soliman (1964) and Albrecht (1967) are important studies of soft structures in the skull. Other morphologic papers are listed under the families below.

The understanding of many parts of the vertebrate skull is made easier by an understanding of cranial development. I have tried to give a brief summary from the literature on the development of each bone in the descriptive sections, but have made no effort to summarize all of cranial development or describe the chondrocranium. I suggest that the following articles be consulted for further development information.

The most detailed study of the fully developed embryonic chondrocranium and its associated ossifications is Kunkel (1912). This study presents excellent figures, including sections and wax model illustrations. Soft parts are also described for the form studied, *Emys orbicularis*. DeBeer (1937, reprinted 1971) has the best summary of the literature and is an excellent introduction to turtle head anatomy. The existence of this work is the main reason that I have not included a developmental summary here. The most important study published since DeBeer's work is that of Pehrson (1945) on the composition of the basisphenoid and this is summarized in the section on that bone.

Other important papers are as follows: Nick (1912) compared chondrocranial features of *Chelydra* and sea turtles and Fuchs (1915) gave a detailed and well-illustrated description of the fully developed chondrocranium in *Eretmochelys*. DeBeer's earlier study (1926) of vertebrate development includes very useful figures and descriptions of the trigemino-facialis region. Shaner's (1926) study of *Chrysemys picta* is one of the few works to illustrate and describe stages preceding and following the fully developed chondrocranium. His figures are most useful in tracing bone development.

The turtle embryology literature is greatly hampered by the lack of taxonomic breadth. Only two families, Emydidae and Cheloniidae,

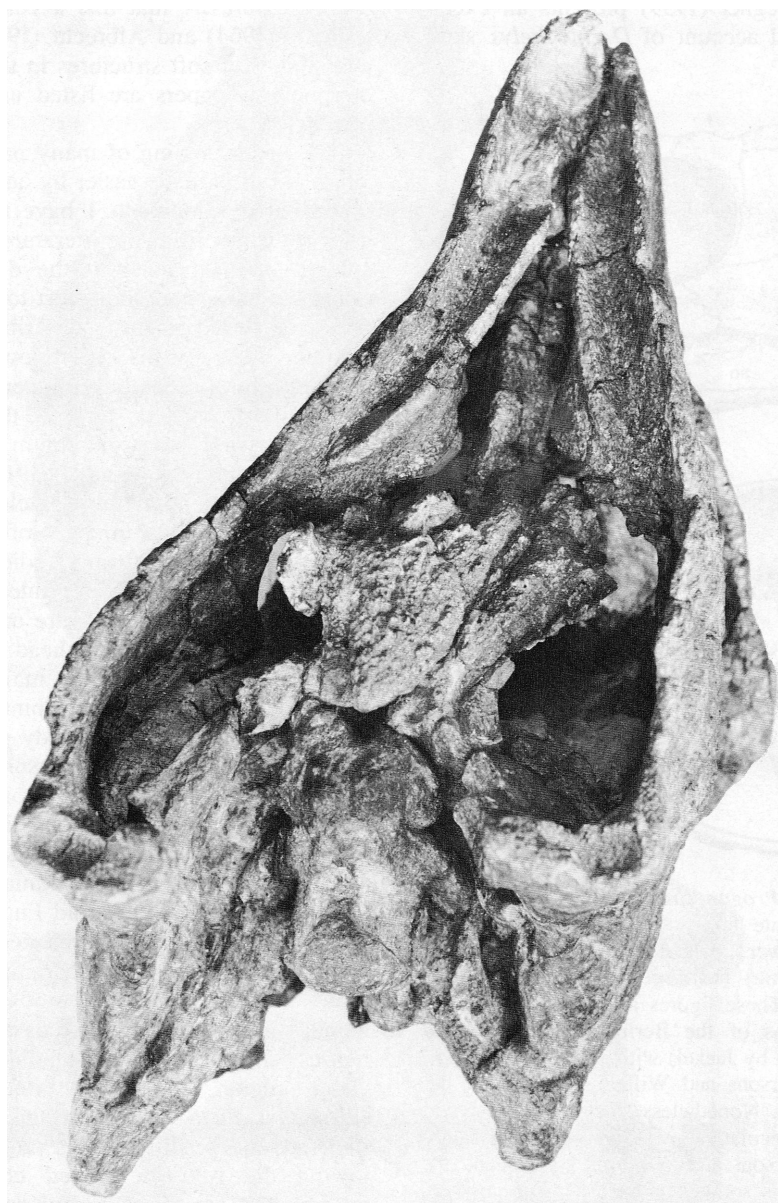


FIG. 117. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. Palatal view of skull described by Jaekel (1916) as *Triassocheilus dux* and synonymized with *Proganochelys quenstedti* by Parsons and Williams (1961). Figure is inadvertently reversed. I am indebted to Drs. Robert Reisz and Robert Carroll for figures 117-119.

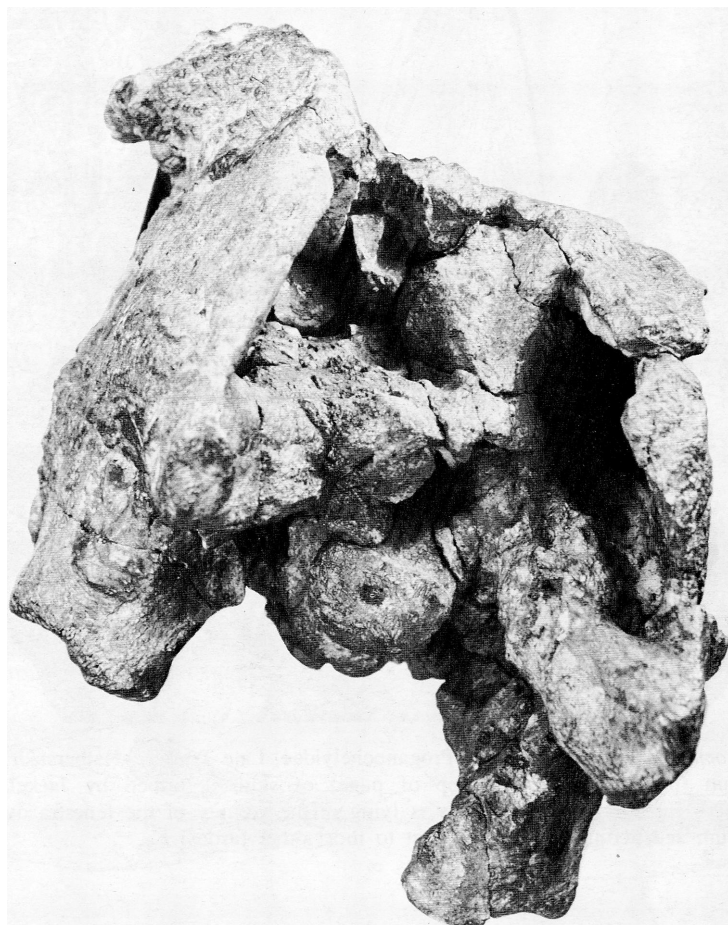


FIG. 118. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. Occipital view of skull described by Jaekel (1916). Figure is inadvertently reversed.

have well-studied representatives and pleurodires are virtually unknown. The only reference I am aware of is Fuchs' (1931) study of lower jaw development in *Podocnemis*.

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER PROGANOCHELYDIA ROMER, 1966

FAMILY PROGANOCHELYIDAE (FIGS. 114-124): Skull characters are described in Jaekel (1916) and Parsons and Williams (1961) but the well-preserved Stuttgart Triassic turtles have never been described. Gaffney (1975d) and Parsons

and Williams (1961) compare known characters with other turtles.

Collins, 1970 (*Proganochelys quenstedti*, ventral and occipital views, interpretations based on Parsons and Williams, 1961, photographs); Jaekel, 1916 (*Proganochelys quenstedti* [*Stegochelys dux*], drawings and photographs of the crushed Berlin specimen); Parsons and Williams, 1961 (*Proganochelys quenstedti*, photographs of skull*)¹; Romer, 1966 (*Progano-*

¹The asterisk (*) indicates that the cited figure is repeated here.



FIG 119. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. Ventral view of basicranium (posterior is toward top of page) of skull described by Jaekel (1916). Figure is inadvertently reversed. End of probe apparently is lying in the vicinity of the fenestra ovalis and shows the relatively open cavum acusticojugulare (in contrast to most other turtles).

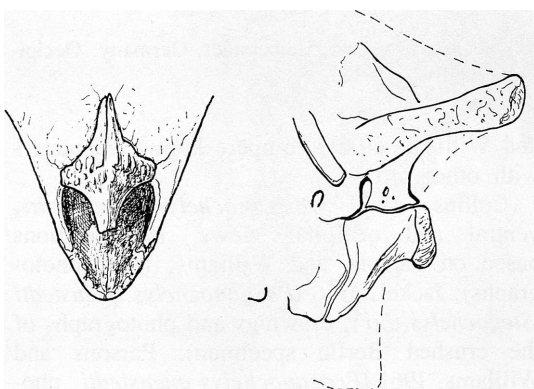


FIG. 120. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. Left, dorsal view of snout showing descending processes of nasals that apparently divide external nares. Right, lateral view of braincase, foramina identification in doubt. From Jaekel (1916).

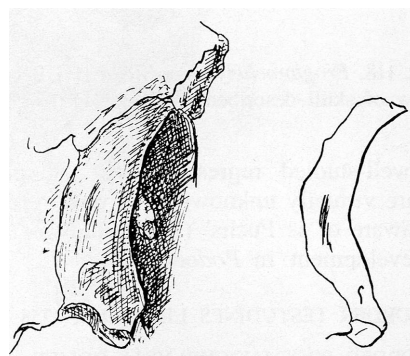


FIG. 121. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. Left quadrate in posterolateral view (left) and lateral view (right). From Jaekel (1916).

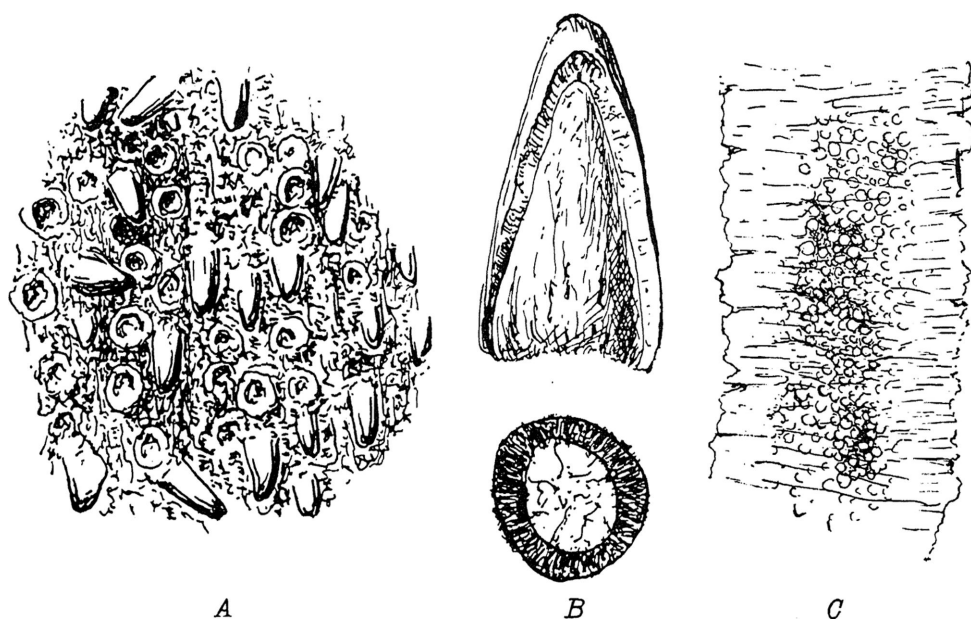


FIG. 122. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. The structure of palatal teeth. A. Part of the upper surface of the parasphenoid on the right and of the pterygoid on the left half of the figure. The suture apparently runs vertically. This figure is X10, but the magnification of the others is not indicated. B. Single tooth showing part of wall broken off (upper) and a cross section (lower). C. Vertical section through dentine (external not indicated). From Jaekel (1916).

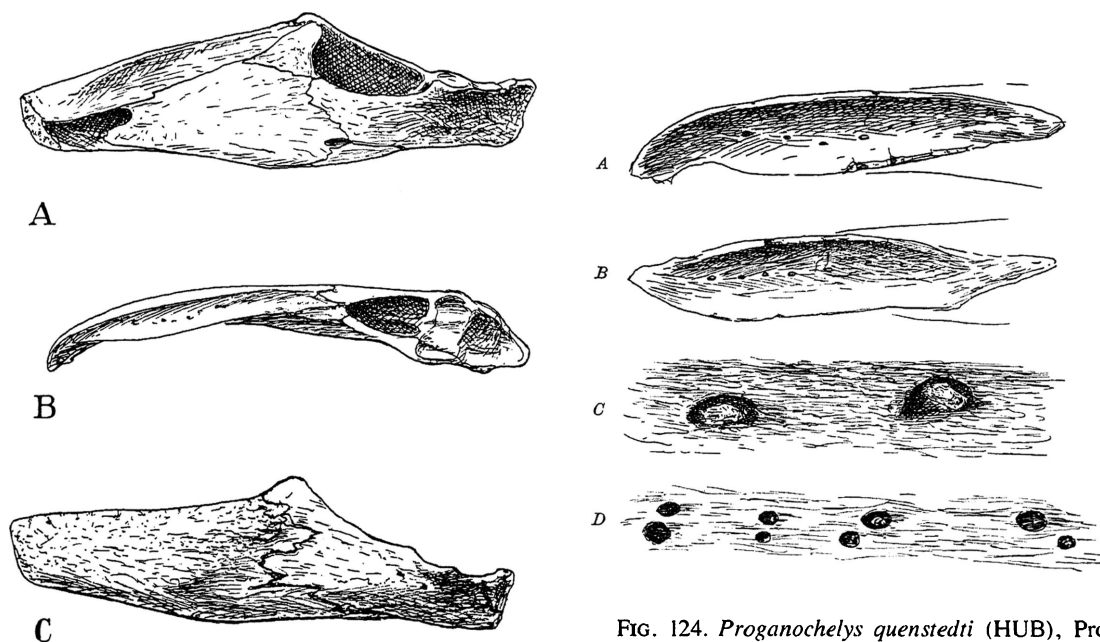


FIG. 123. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. A. Medial view of right lower jaw ramus; B. Dorsal view of right ramus; C. Lateral view of left ramus. From Jaekel (1916).

FIG. 124. *Proganochelys quenstedti* (HUB), Proganochelyidae, Late Triassic, Halberstadt, Germany. A, B. Lower jaw showing "dental pulp cavities." C. Two of these X20. D. Maxillary "dental pulp cavities" X10. From Jaekel (1916). It was presumed by Jaekel that these structures were rudimentary teeth of some sort.

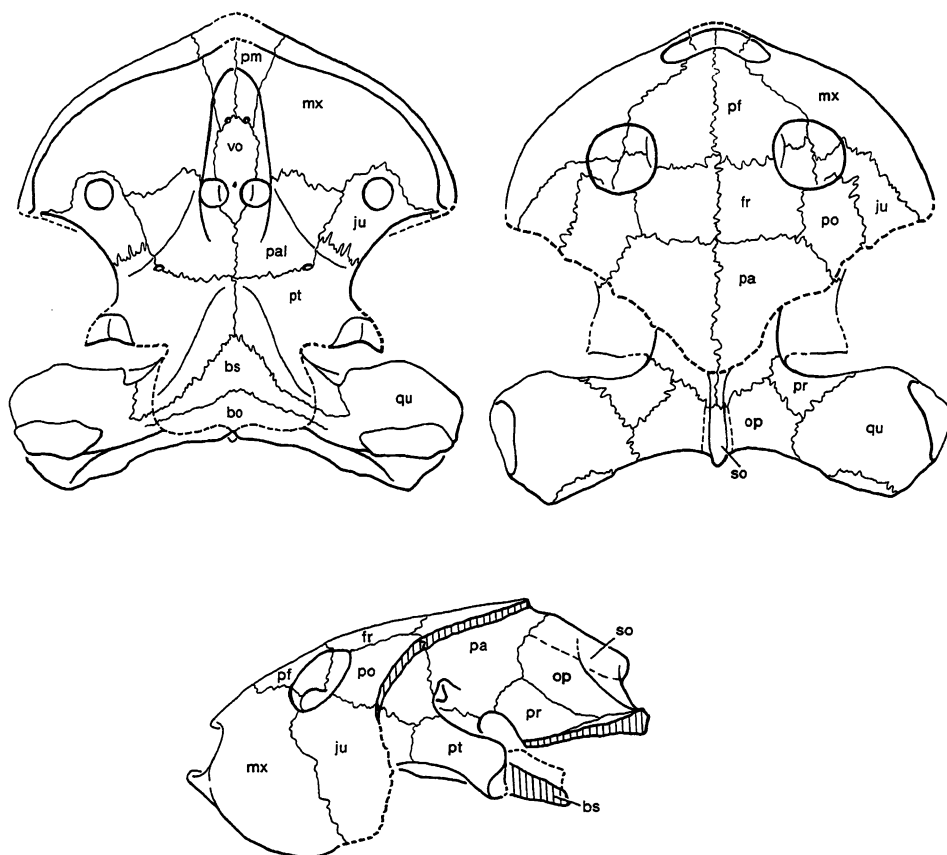


FIG. 125. *Bothremys cooki* (AMNH 2521; as preserved 69 mm.), Pelomedusidae, Hornerstown Formation, Late Cretaceous (?), Tinton Falls, New Jersey. Otic regions restored from FMNH PR 247, *Bothremys barberi*, Mooreville Tongue, Selma Formation, Late Cretaceous, Harrell, Dallas County, Alabama. See Gaffney and Zangerl (1968) for description and other figures.

chelys quenstedti, side and palatal restorations, see Gaffney, 1975d for comments).

SUBORDER CASICHELYDIA GAFFNEY, 1975a

INFRAORDER PLEURODIRA (COPE, 1868)

FAMILY PELOMEDUSIDAE (FIGS. 125-141): There is no single review of cranial osteology for either living or fossil pelomedusids. Merwe (1940) comes closest to a thorough description but the most detailed study is that of a highly derived form, *Bothremys*, (Gaffney and Zangerl, 1968). Gray (1873c), Williams (1954a,

1954b, 1954c), Wood (1970), Mittermeier and Wilson (1974), Albrecht (1976) and Gaffney (1977b) also presented important contributions to the sparse pelomedusid skull literature.

I have followed Baur (1890) and Williams (1954b, 1954c) in retaining *Erymnochelys madagascariensis* and *Peltocephalus dumeriliana* distinct from *Podocnemis*. I also use Laurent (1965 and others cited by him) for *Pelusios*, and Loveridge (1941) for *Pelomedusa*. Another important paper on pelomedusid systematics is Siebenrock (1902).

Albrecht, 1976 (*Podocnemis unifilis*, *Pelomedusa subrufa*); Andrews, 1906 (*Stereogenys*

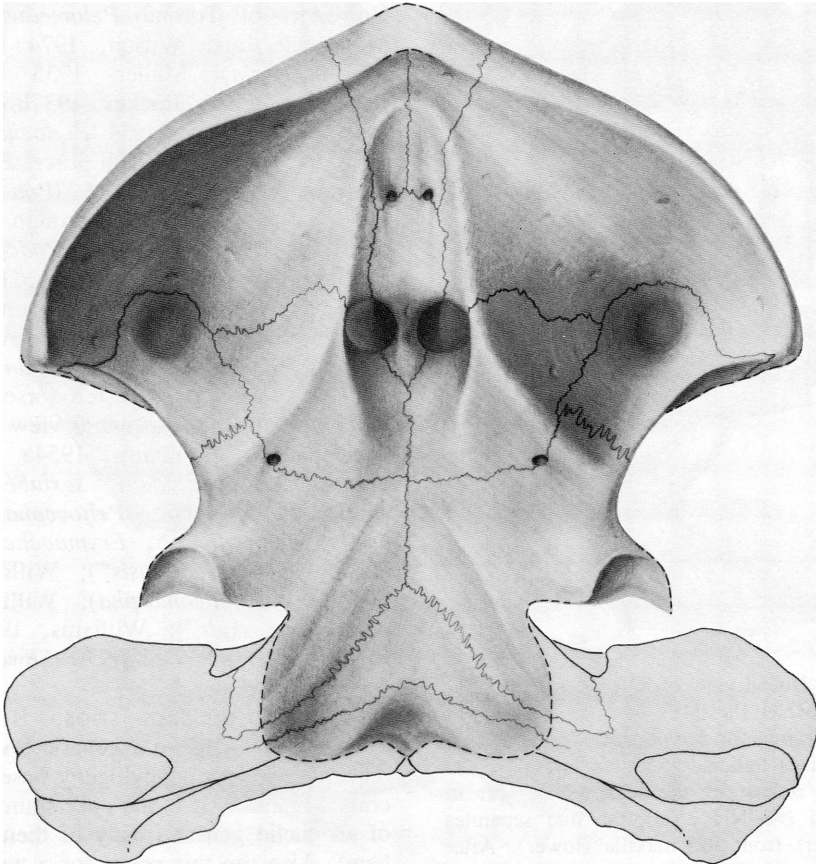


FIG. 126. *Bothremys cooki* (AMNH 2521), Pelomedusidae, Hornerstown Formation, Late Cretaceous (?), Tinton Falls, New Jersey. Palatal view, shaded portion slightly restored, limits of processus trochlearis pterygoidei hypothetical. Quadrates and posterolateral (unshaded) regions restored from a partial skull of *Bothremys barberi* (FMNH PR 247). Skull length as preserved 69 mm. See Gaffney and Zangerl (1968) for description and other figures. From Gaffney (1977b).

cromeri); Bergounioux and Crouzel, 1968 ("Potamochelys" gigantea¹); Boulenger, 1889 (*Pelomedusa subrufa* [galeata], repeated in Wermuth and Mertens, 1961); deBroin, 1971

¹This is a pelomedusid skull from the Early Cretaceous of Niger currently being studied by F. de Broin of Paris and is the oldest pelomedusid skull I am aware of. The name is preoccupied by *Potamochelys* Fitzinger, 1843.

(?Roxochelys vilavilensis); Dacqué, 1912 (*Dacquemys paleomorpha** [Stereogenys libyca]); Fuchs, 1931 (*Podocnemis expansa*, detailed figures of lower jaw anatomy in embryos and adults, ventral view of basicranium, sections through embryo in region of mandibular articulation); Gaffney and Zangerl, 1968 (*Bothremys cooki**, *B. barberi**, *Podocnemis unifilis*); Gaffney, 1975d (*Podocnemis expansa*, series of

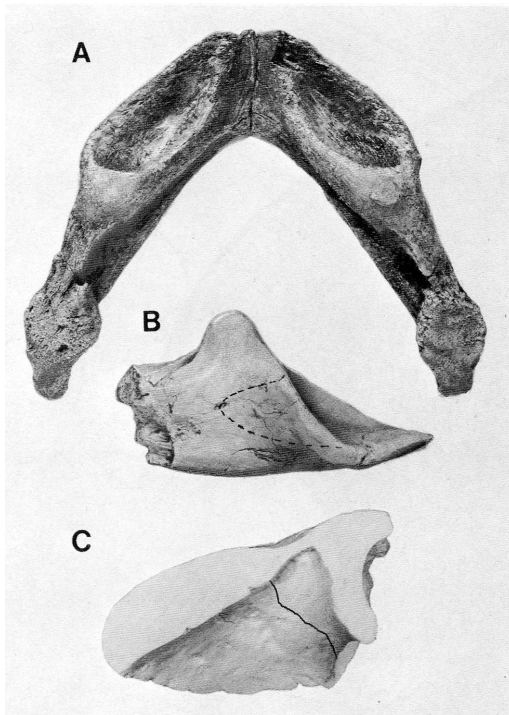


FIG. 127. A. Dorsal view of lower jaw of *Bothremys barberi* (FMNH PR 247). B. Lateral view of left lower jaw ramus in *Bothremys cooki* (AMNH 2521), dashed lines indicate extent of pit. C. Cross section through a cast of the right palatal pit in *Bothremys cooki* (AMNH 2521), the line separates the jugal (upper) from the maxilla (lower). After Gaffney and Zangerl (1968); *q.v.* for further figures and description.

transverse sections, *Pelomedusa subrufa*, pterygoid*); Gaffney, 1977b (*Bothremys* sp., endocast, palate); Gray, 1855 (*Podocnemis expansa**, repeated in Wermuth and Mertens, 1961); Gray, 1870b (*Podocnemis sextuberculata* [*Bartlettia pitipii*], repeated in Boulenger, 1889, and Wermuth and Mertens, 1961); Gray, 1873c (*Pelusios niger* [*Sternothaerus*], repeated in Boulenger, 1889, and Wermuth and Mertens, 1961); Hay, 1908a (*Bothremys cooki*, a particularly good halftone of *Podocnemis expansa*, which is repeated as a line drawing in Gregory, 1946); Hewitt, 1927 (*Pelusios sinuatus*); Merwe, 1940 (*Pelomedusa subrufa* [galeata], good figures including occiput, sections*

through ear have inaccurate labels and are reproduced here but relabeled on the basis of University of Toronto *Pelomedusa* sections); Mittermeier and Wilson, 1974 (*Podocnemis erythrocephala*); Müller, 1935 (*Podocnemis vogli*, *P. unifilis*); Ruckes, 1937b (*Podocnemis expansa**); Schwarz, 1934 (*Podocnemis unifilis*, embryos sectioned through processus trochlearis pterygoidei); Shiino, 1913 (*Podocnemis expansa*, embryo sectioned through central portion of head); Shindo, 1914 ("Podocnemis" sp., schematic arteries); Siebenrock, 1897 (*Erymnochelys madagascariensis*, sagittal section, oblique view of ear, lateral view of skull); Suarez, 1969 (*Podocnemis elegans*); Wegner, 1959 (*Pelusios niger*, posterodorsolateral view; *Podocnemis expansa*, ventral view of disarticulated parietal); Williams, 1954a (*Podocnemis expansa**, *P. unifilis**, *P. sextuberculata**, *P. vogli**, *P. lewyana**, *Peltocephalus* [*Podocnemis*] *dumeriliana**, *Erymnochelys* [*Podocnemis*] *madagascariensis**); Williams, 1954b (*Dacquemys paleomorpha*); Williams, 1954c ("Moghara skull"); Williams, 1956 (*Podocnemis bassleri*); Wood, 1970 (*Shweboemys pilgrimi*; *S. gaffneyi*).

FAMILY CHELIDAE (FIGS. 110, 142-150): Gaffney (1977a) gave a generic level review of the Chelidae and a phylogeny based largely on cranial features. It is the only source for figures of all chelid genera (many of them reproduced here). Also see this paper for a more complete literature survey. Other useful works for chelid systematics are Boulenger (1889), Zangerl and Medem (1958), Goode (1967), Burbidge et al. (1974), Cogger (1975), and Rhodin and Mittermeier (1976). There is no detailed description of a chelid skull in the literature although Albrecht (1976) provided a useful description of the cranial arteries and foramina in chelids.

Albrecht, 1976 (*Phrynops* [*Batrachemys*] *nasuta*, arteries and canals); Boulenger, 1889 (*Chelus fimbriata*, *Batrachemys* [*Rhinemys*] *nasuta*, *Phrynops geoffroanus* [*Hydraspis hilarii*], *Elseya dentata*, repeated in Goode, 1967); Burbidge et al., 1974 (*Pseudemys dura* *umbrina*, *Emydura* [*Elseya*] *latisternum*, *Emydura macquarrii*, *Chelodina oblonga*); Fuchs, 1931 (*Chelus fimbriata*, lower jaw); Gaffney,

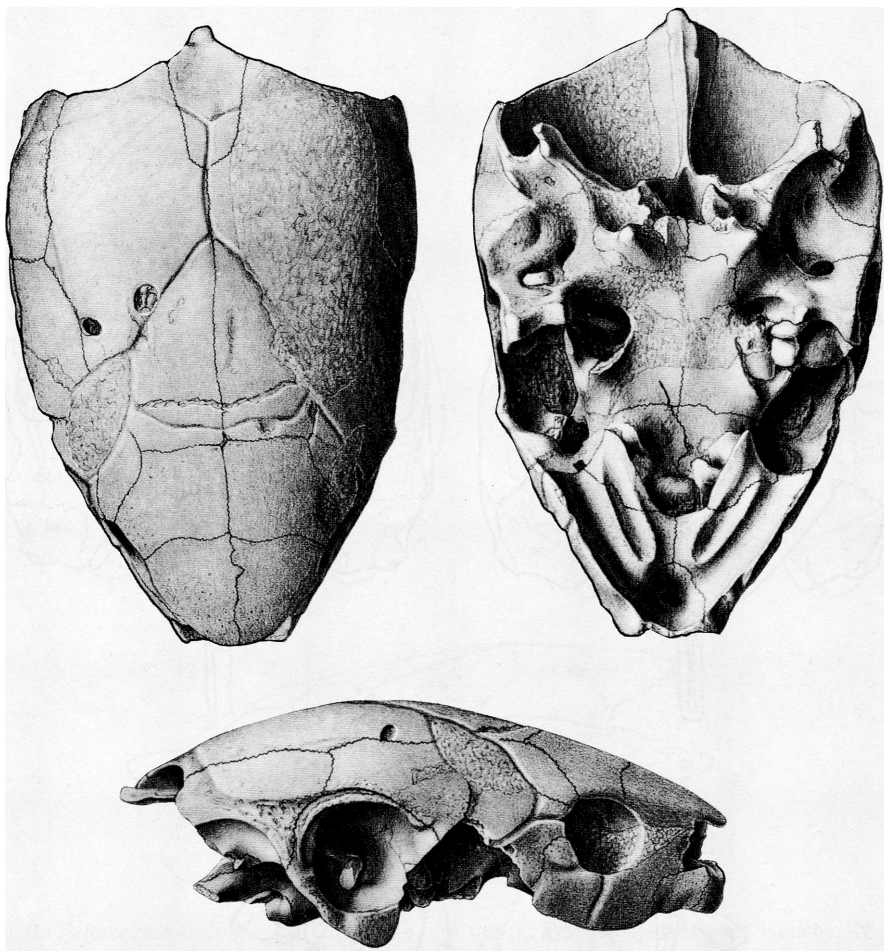


FIG. 128. *Dacquemys paleomorpha* (Staatliches Museum für Naturkunde, Stuttgart, 12645, estimated length 72 mm.), Pelomedusidae, Lower Oligocene, Diieh, Fayum of Egypt. Dorsal view on left, palatal view on right, lateral view below. From Daqué (1912); for further description and other figures also see Williams (1954b).

1975d (*Chelodina* sp.*, *Emydura* cf. *australis**); Gaffney, 1977a (*Chelodina novaeguineae*, *Chelodina expansa**, *Chelus fimbriata**, *Elseya latisternum*, *Emydura macquarrii**, *Hydromedusa tectifera**, *Phrynops geoffroanus**, *Phrynops gibba**, *Platemys platycephala**, *Pseudemydura umbriana**); Goode, 1967 (*Chelodina longicollis*, *C. expansa*, *Emydura macquarrii*, *Pseudemydura umbrina*); Gray, 1869 (*Chelodina oblonga* [collei], repeated in Gray, 1870a, Boulenger, 1889, and Wermuth and Mertens, 1961); Gregory, 1946 (*Chelus*

fimbriata); Hay, 1908a (*Hydromedusa* sp., palate only); Hoffman, 1890 (*Emydura* sp. [*Chelymys victoria*], *Chelodina longicollis*, *Chelus fimbriata*); Peters, 1839 (*Hydromedusa maximiliani*); Siebenrock, 1897 (*Chelus fimbriata*, sagittal and oblique view of ear; *Chelodina longicollis*, internal views of cavum labyrinthicum*, pterygoid, and basisphenoid*; *Platemys* [*Hydraspis*] *radiolata*, oblique view of ear); Waite, 1929 (*Chelodina longicollis*); Zangerl and Medem, 1958 (*Batrachemys dahli**).

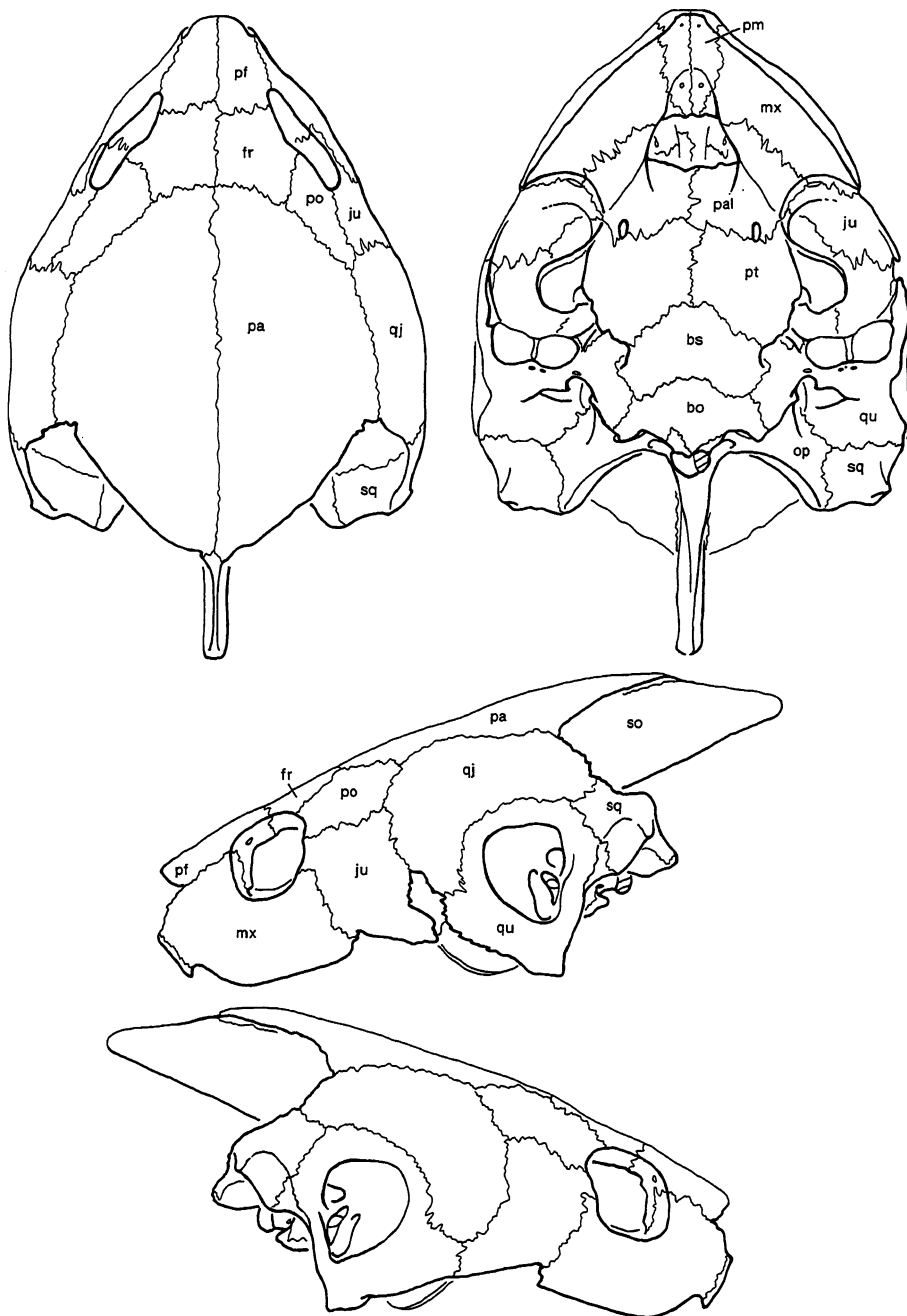


FIG. 129. *Erymnochelys madagascariensis* (Museum National d'Histoire Naturelle, Paris, 92.494, DD67), Pelomedusidae, Malagasy Republic. Note injury to condylus occipitalis (apparently during life) and anomalous separation of quadrate and jugal on left side.

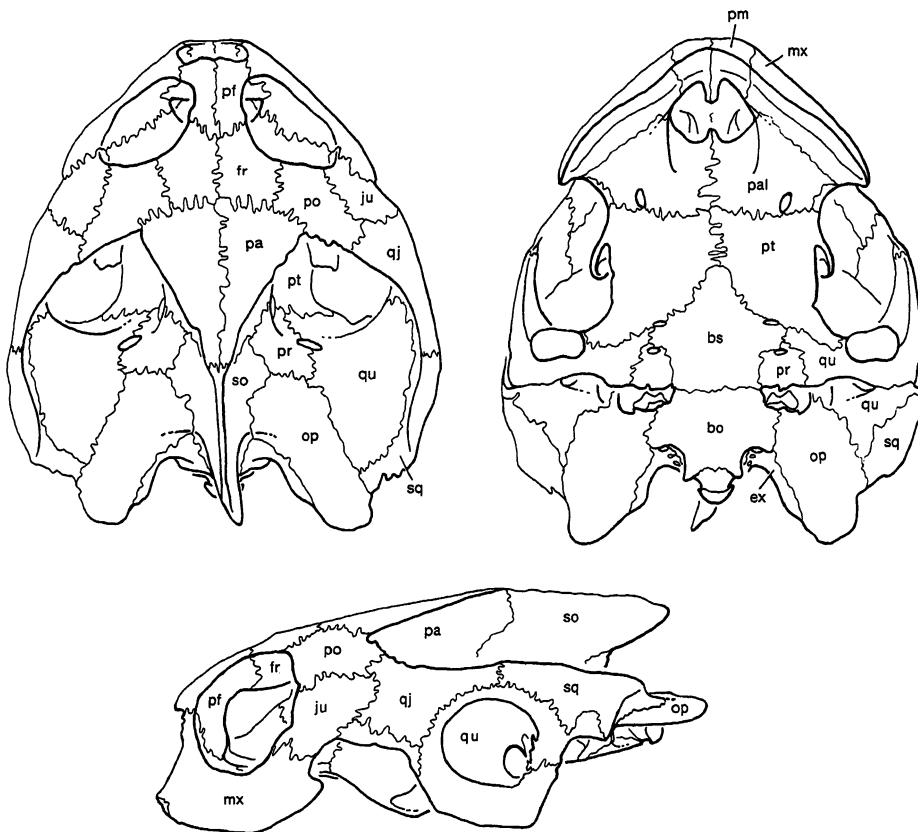


FIG. 130. *Pelomedusa subrufa* (MCZ 134434, 38 mm.), Pelomedusidae, near Katsina, Nigeria. "Extra" cheek bone is a variation found only on the left side of this specimen.

INFRAORDER CRYPTODIRA (COPE, 1868)

PARVORDER PARACRYPTODIRA GAFFNEY, 1975d

SUPERFAMILY BAENOIDEA WILLIAMS, 1950a

FAMILIES GLYPTOPSIDAE AND BAENIDAE (FIGS. 151-164): No detailed cranial study is currently available for a baenid (although Gaffney, 1969, contains a comparative description of baenid skulls, this work cannot be considered widely available). See Gaffney (1972a) for family diagnosis, systematics, and comparative table of Glyptopsidae and Baenidae. Evans and Kemp (1975) provided a good description with figures for the glyptopsid, *Mesochelys*, and they later described *Dorsetochelys*, a baenid.

I follow the classification presented in Gaffney (1972a).

Evans and Kemp, 1975 (*Mesochelys durlstonensis*, overall views* as well as sagittal section, basicranium and disarticulated elements); Evans and Kemp, 1976 (*Dorsetochelys delairi*); Gaffney, 1972a (*Trinitichelys hiatti**, *Hayemys latifrons**, *Plesiobaena antiqua**, *P. putorius*, *Eubaena cephalica**, *Stygiochelys estesi**, *Palatobaena bairdi**, *Baena arenosa**, *Chisternon undatum**, most of these are represented by stereophotographs of palates as well as line drawings); Gaffney, 1975d (*Eubaena cephalica**), Hay, 1908a (*Chisternon undatum [hebraicum]*, *Eubaena cephalica*, *Baena*

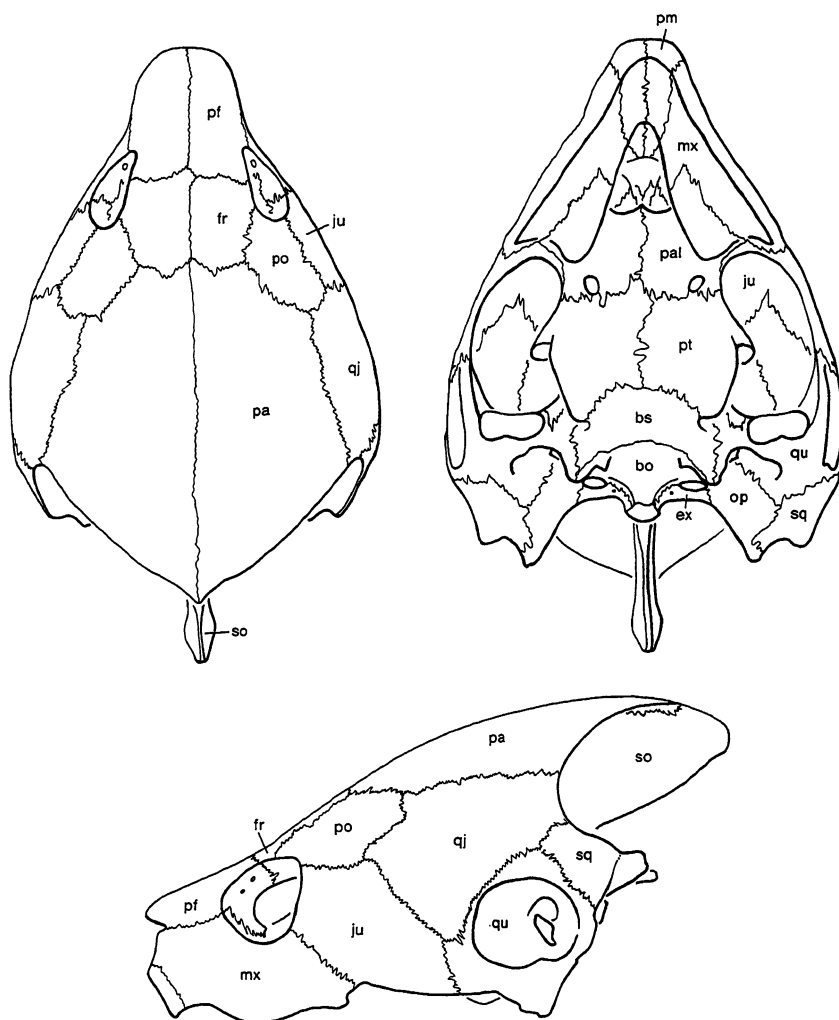


FIG. 131. *Peltocephalus dumeriliana* (MCZ 93077, 108 mm.), Pelomedusidae, Lago Jacaré, Rio Trombetas, Para, Brazil.

arenosa [*riparia*, *sima*], *Hayemys* [*Eubaena*] *latifrons*, *Glyptops plicatulus*).

PARVORDER EUCRYPTODIRA GAFFNEY, 1975a

SUPERFAMILY TRIONYCHOIDEA FITZINGER, 1826¹

¹In my first use of Trionychoidea and Testudinoidea (1975d) I was unaware that Fitzinger had used these terms before Gray, 1870a, and Baur, 1893, respectively. I take this opportunity to correct this error.

FAMILIES KINOSTERNIDAE (FIGS. 165-170) AND DERMATEMYDIDAE (FIGS. 171-172): Bienz (1895) provided a description of *Dermatemys*, Williams (1952b) described the fossil kinosternid *Xenochelys*, and McDowell (1964) commented on cranial characters of *Dermatemys*. A systematically interesting description of the cranial canals, foramina, and arteries is in Albrecht (1967) and much of his material is

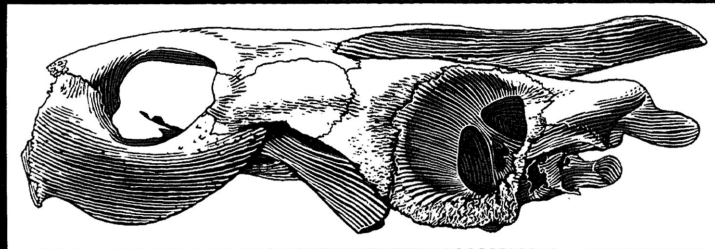
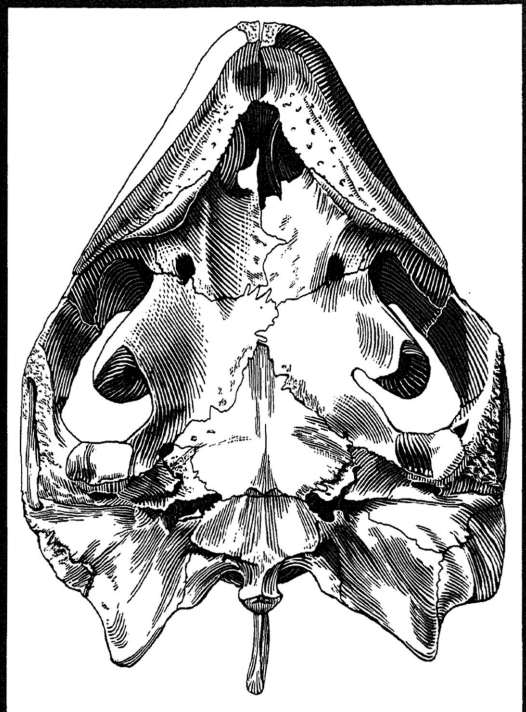
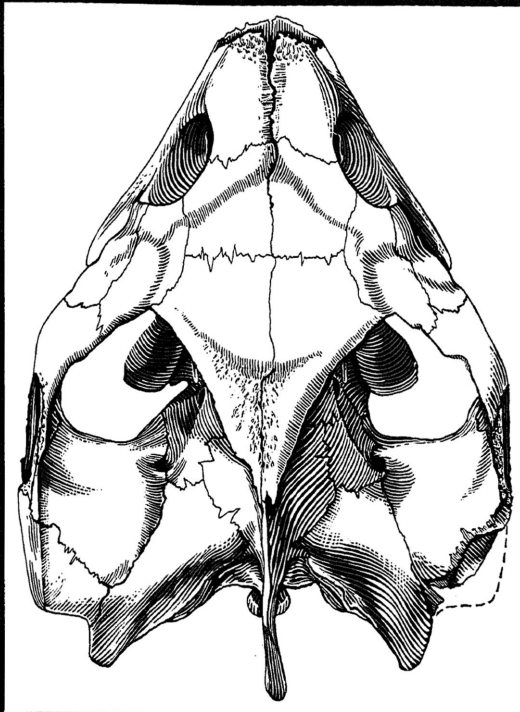


FIG. 132. *Pelusios niger* (MCZ 53627), Pelomedusidae, "West Africa." I am indebted to Drs. E. E. Williams and R. Wood for the use of these previously unpublished drawings.

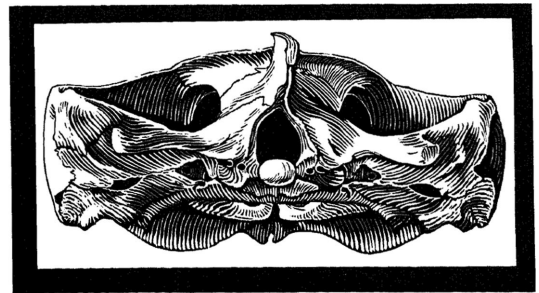
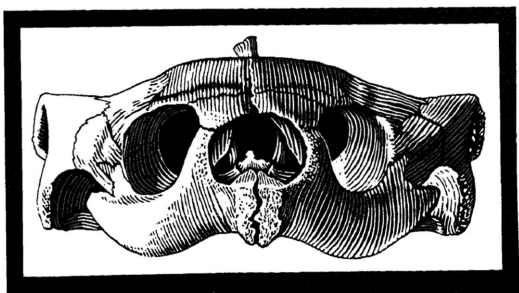


FIG. 133. *Pelusios niger* (MCZ 53627), Pelomedusidae, "West Africa."

discussed in this paper. A brief description of the fossil dermatemydid *Baptemys* can be found in Hay (1908a), and McDowell (1961) supplied information on arterial foramina.

The Family Dermatemydidae includes many

shell genera of dubious affinities and here I have only considered *Basilemys* and *Baptemys* (on the basis of basicranial and palatal characters) as members. For the kinosternids I follow Wermuth and Mertens (1961) but the reader

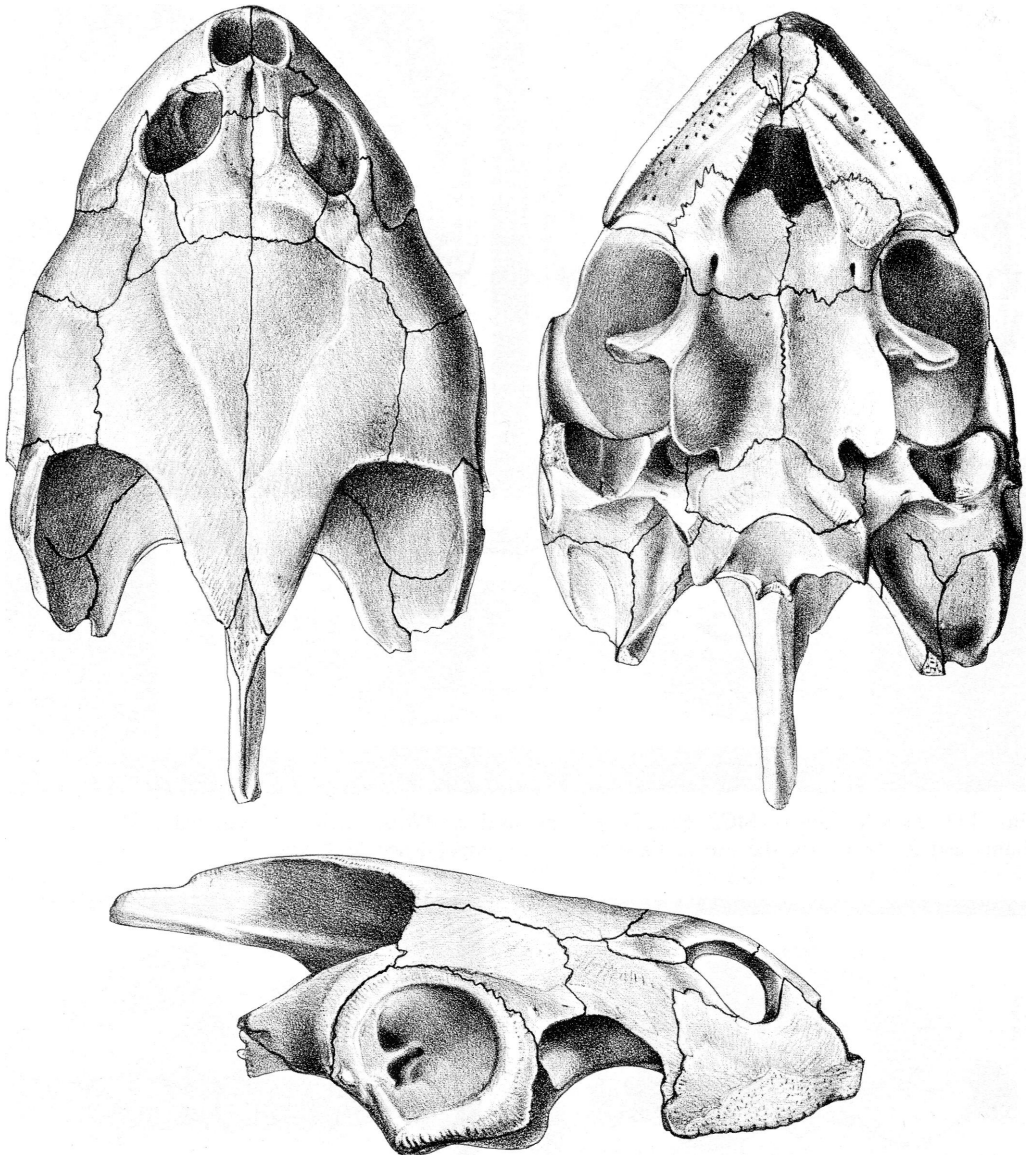


FIG. 134. *Podocnemis expansa*, Pelomedusidae. From Gray (1855), modified by the addition of sutures.

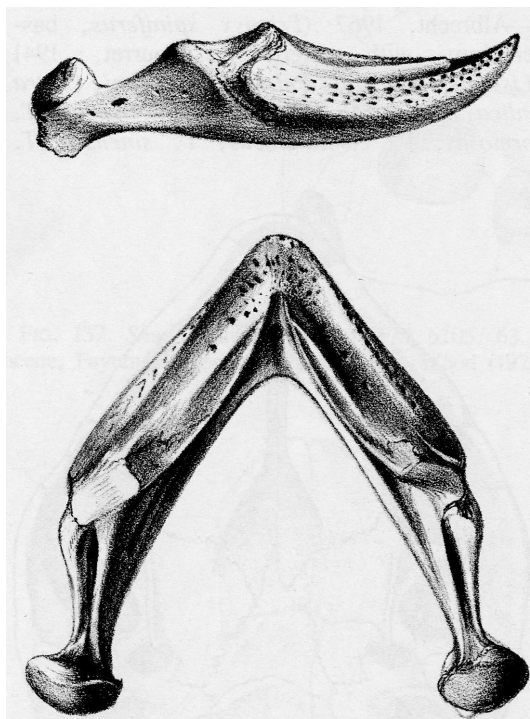


FIG. 135. *Podocnemis expansa*, Pelomedusidae. Lateral (upper) and dorsal (lower) views of lower jaw. From Gray (1855).

should also see Siebenrock (1907), Williams (1952b), Tinkle (1958), and Ernst and Barbour (1972) for further information.

Albrecht, 1967 (*Sternotherus odoratus*, arteries*); Bienz, 1895 (*Dermatemys mawii*, good halftones of skull including lower jaws and ethmoid region); Boulenger, 1889 (*Kinosternon* [*Cinosternum*] *leucostomum*, repeated in Wermuth and Mertens, 1961); Ernst and Barbour, 1972 (*Sternotherus odoratus*, *S. carinatus*, *S. minor*, *Kinosternon subrubrum*, *K. baurii*, *K. flavescens*, *K. sonoriense*, *K. hirtipes*; all are photographs with more or less indistinct sutures); Feuer, 1970 (*Staurotypus triporcatus*, *Sternotherus odoratus*, *Kinosternon flavescens*, dorsal and occipital views only of latter two; figures crude and inaccurate); Gray, 1869

(*Staurotypus salvinii*, repeated in Boulenger, 1889, and Wermuth and Mertens, 1961); McDowell, 1961 (*Kinosternon sonoriense*, arteries in a horizontal section of skull); McDowell, 1964 (*Dermatemys mawii**); Schwarz, 1934 (*Kinosternon subrubrum*, figure of embryo sectioned through processus pterygoideus externus); Siebenrock, 1897 (*Sternotherus odoratus* [*Cinosternum odoratum*], sagittal section and basisphenoid; *Staurotypus salvinii*, oblique view of ear and dorsal view of pterygoid); Siebenrock, 1907 (*Sternotherus odoratus* [*Cinosternum odoratum*], *Kinosternon subrubrum* [*Cinosternum steindachneri*, *C. pensilvanicum*], *Kinosternon* [*Cinosternum*] *flavescens*, *K. [C.] leucostomum*, *K. [C.] cruentatum*; all are good half tones but only of palate); Tinkle, 1958 (diagrammatic views of *Sternotherus carinatus*, *S. minor*, and *S. depressus*); William, 1952b (*Staurotypus salvinii**, *Xenochelys formosa**).

FAMILIES TRIONYCHIDAE (FIGS. 176-186) AND CARETTOCHELYIDAE (FIGS. 173-175): Ogushi (1911) has provided one of the most useful single species descriptive accounts for a turtle skull. His later paper (Ogushi, 1913) supplied considerable information on soft structures but it does not compare with the earlier in terms of cranial morphologic illustrations. Siebenrock (1897) and Albrecht (1967) are also particularly important for trionychid skull morphology. Nearly all the species recognized by Wermuth and Mertens (1961) are represented in the literature by usable skull figures; see especially Gray (1855, 1864, 1873a), Bourret (1941), and Loveridge and Williams (1957), but some caution is necessary in accepting retrospective identification of specimens figured many years ago. *Carettochelys* has been figured and described by Walther (1922) but no detailed internal anatomy has appeared.

Trionychid systematics has usually been approached regionally; Loveridge and Williams (1957) being the only work dealing with a regional fauna in the context of a worldwide phylogenetic hypothesis. Other important taxonomic treatments useful in dealing with recent trionychids are Gray (1864, 1873a), Siebenrock (1902), de Rooij (1915), Smith (1931), Bourret

(1941), Stejneger (1944), Webb (1962), and Dalrymple (1977, for cranial variation in *Trionyx*). Fossil trionychid memoirs are Hay (1908a) for North America, and Hummel (1929) for the world. In this paper I have followed Wermuth and Mertens (1961) for Trionychidae

and Carettochelyidae.

Albrecht, 1967 (*Trionyx spiniferus*, basicranium with arteries*), Bourret, 1941 (*Lissemys punctata*, *Pelochelys bibroni*, *Chitra indica*, *Dogania subplana*, *Trionyx hurum*, *T. formosus*, *T. cartilagineus*, *T. sinensis*, *T.*

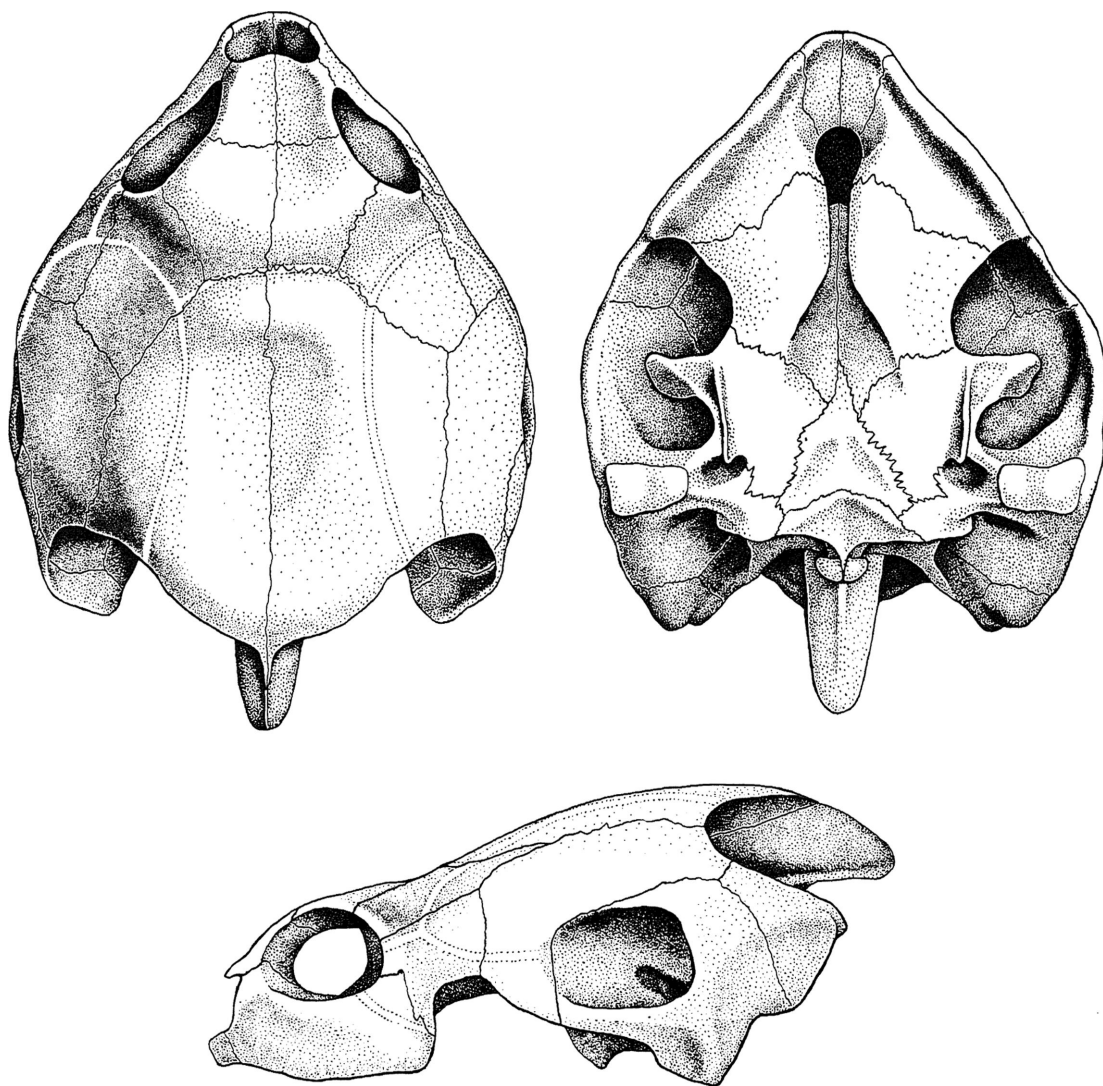


FIG. 136. *Shweboemys antiqua* (YPM 6205, 63 mm.), Pelomedusidae, Qasr el-Sagha Formation, late Eocene, Fayum Depression, Egypt. From Wood (1971); I am indebted to Dr. R. Wood for the use of these figures, which were drawn under his direction.

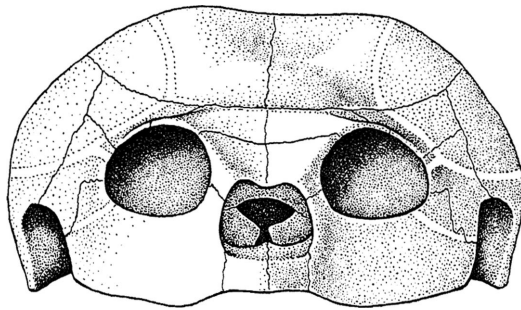


FIG. 137. *Shweboemys antiqua* (YPM 6205, 63 mm.), Pelomedusidae, Qasr el-Sagha Formation, late Eocene, Fayum Depression, Egypt. From Wood (1971).

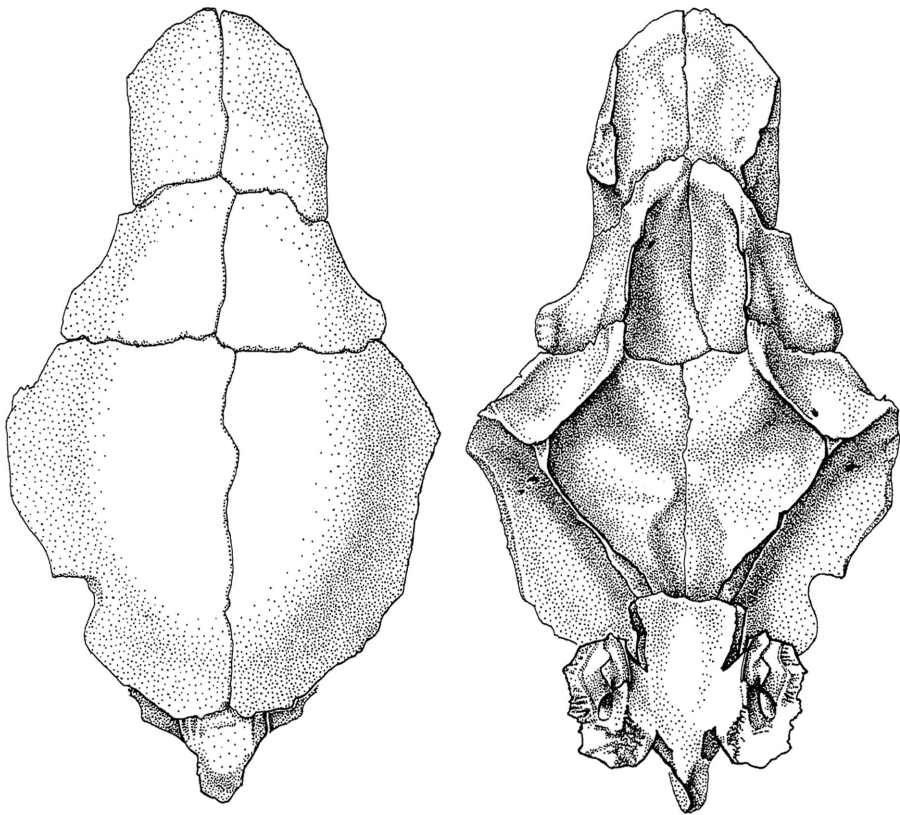


FIG. 138. *Taphrosphys sulcatus* (Academy of Natural Sciences, Philadelphia, 15544, length as preserved 77 mm.), Pelomedusidae, Hornerstown Formation, Late Cretaceous, Sewell, New Jersey. Skull roof consisting only of prefrontals, frontals, parietals, and supraoccipital. Dorsal view left, ventral view right. See Gaffney (1975a).

steindachneri; these are for the most part lateral and ventral views of variable quality, most are too small for detailed sutural definition); Dalrymple, 1977 (*Trionyx ferox*, *T. spiniferus*, *T. cartilagineus*); Deraniyagala, 1939 (*Lissemys punctata*); Eiselt, 1976 (*Trionyx triunguis*, *T.*

euphraticus); Ernst and Barbour, 1972 (*Trionyx muticus*, *T. spiniferus*, *T. ferox*, *T. sinensis*, all are photographs of mostly good quality but sutures are indistinct); Fang, 1934 (*Pelochelys bibroni* [cantorii]); Gilmore, 1934 (*Trionyx* [*Amyda*] *gregaria*); Girgis, 1964 (*Trionyx tri-*

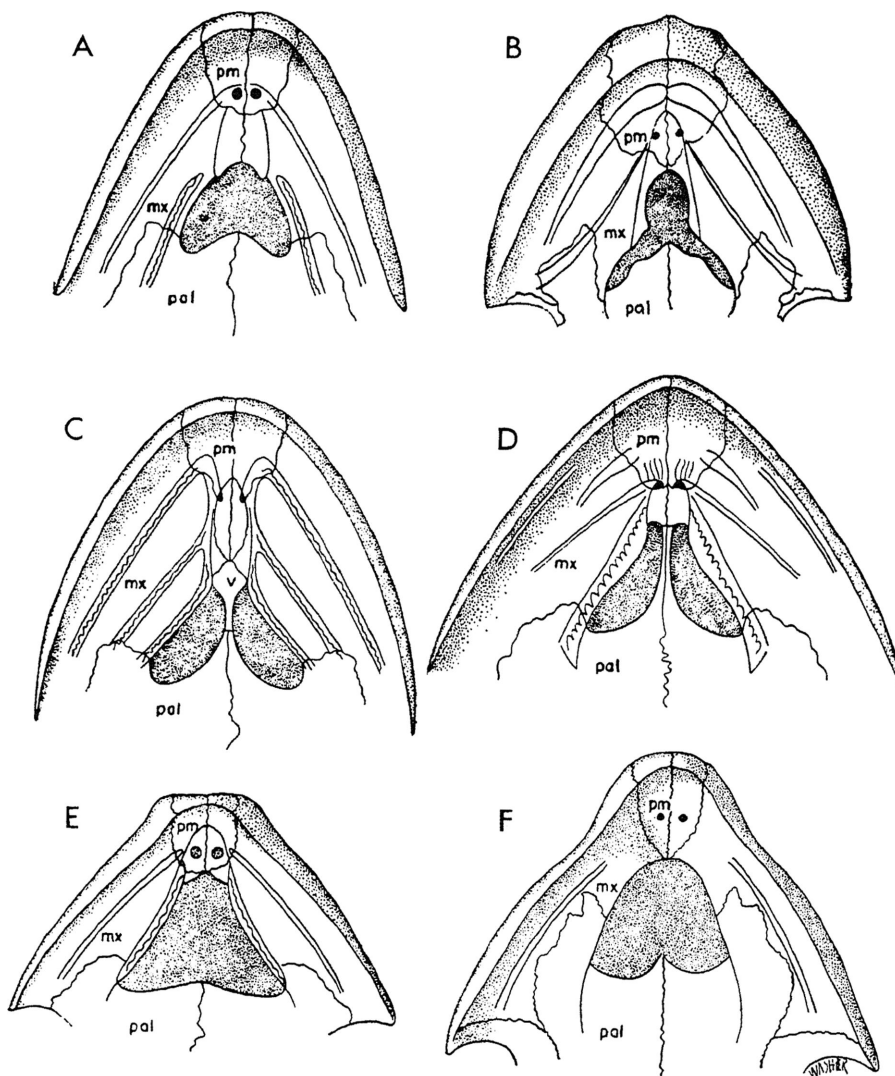


FIG. 139. Semidiagrammatic views of the triturating surfaces in species usually placed in the genus *Podocnemis*. Here, however, I use two genera of Baur (1890) and the species assignments differ from Williams (1954a). A. *Podocnemis unifilis*. B. *Podocnemis lewyana*. C. *Podocnemis vogli*. D. *Podocnemis expansa*. E. *Erymnochelys madagascariensis*. F. *Peltocephalus dumeriliana*. From Williams (1954a).

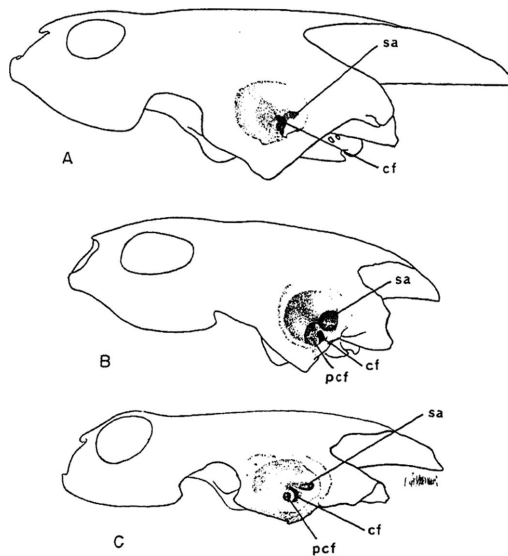


FIG. 140. Lateral views of pelomedusid skulls showing terminology of structures in cavum tympani. A. *Podocnemis expansa*; B. *Erymnochelys madagascariensis*; C. *Podocnemis unifilis*. cf, incisura columellae auris; pcf, precolumellar fossa; sd, antrum postoticum. From Williams (1954a).

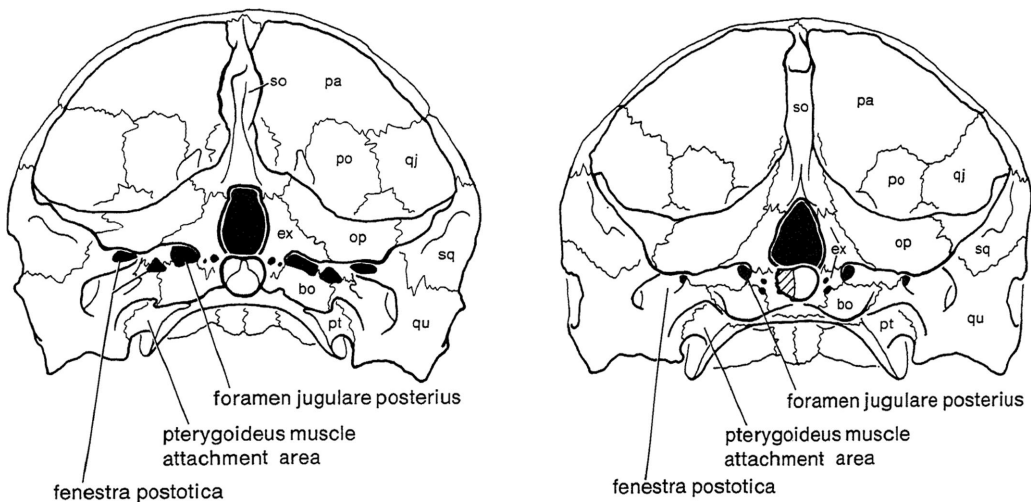


FIG. 141. Occipital views of recent Pelomedusidae. Left, *Peltoccephalus dumeriliana* (MCZ 93077); right, *Erymnochelys madagascariensis* (Museum National d'Histoire Naturelle, Paris, 92.494,DD67). Both of these species are referred to *Podocnemis* by Boulenger (1889), Williams (1954a), Wermuth and Mertens (1961).

unguis, cranial arteries); Gray, 1855 (*Chitra indica**, *Trionyx gangeticus*; the two above are repeated in Wermuth and Mertens, 1961; *Trionyx triunguis* [*niloticus*], these are good quality halftones but some sutures are missing or ambiguous); Gray, 1864 (*Dogania subplana*, *Trionyx cartilagineus* [*Aspilus carniferus*], *Lissemys punctata* [*Potamochelys stellatus*], *Pelochelys bibroni* [*cantorii*], *Chitra indica*,

Cycloderma aubryi [*Heptathyra frenata*], *Cyclanorbis senegalensis* [*Cyclanosteus senegalensis*], many of these reappear in Boulenger, 1889, and Wermuth and Mertens, 1961); Gray, 1869 (*Trionyx cartilagineus* [*jeudi*]); Gray, 1873a (*Trionyx triunguis* [*Fordia africana*], *T. formosus* [*Nilssonina formosa* and *Isola pequensis*], *T. leithii*, *T. [Callinia] spiniferus*, *T. muticus* [*Callinia microcephala*], *T. [Rafetus]*

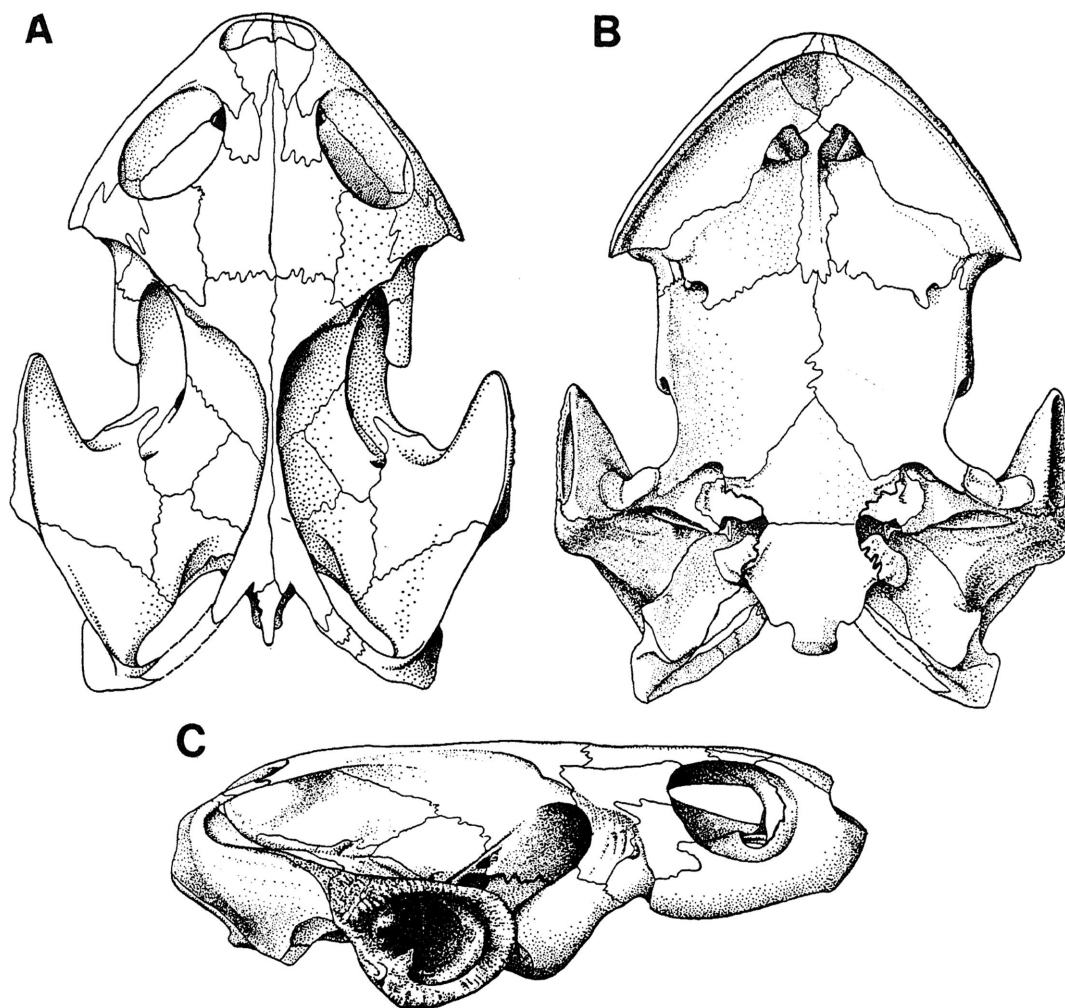


FIG. 142. *Batrachemys dahli* (FMNH H 75980, 53 mm.), Chelidae, vicinity of Sincelejo, Bolivar, Columbia. From Zangerl and Medem (1958) with modifications from specimen. Referred to *Phrynops* subgenus *Batrachemys* by Zangerl and Medem (1958).

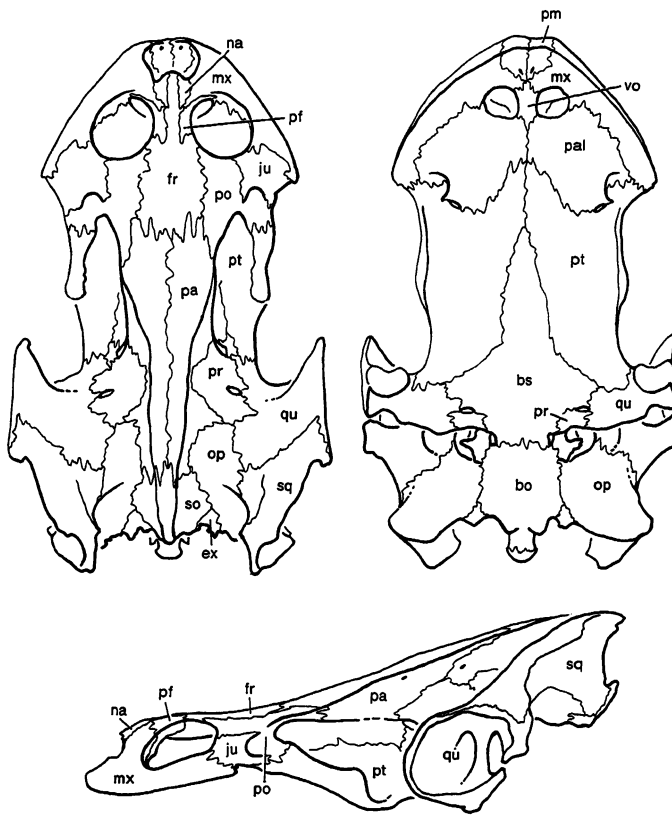


FIG. 143. *Chelodina expansa* (AMNH 108948), Chelidae, Echuca, Victoria, Australia. From Gaffney (1977a).

euphraticus; *T. muticus* appears in Boulenger, 1889, and others appear in Wermuth and Mertens, 1961); Hay, 1908a (*Trionyx* [*Platypeltis*] *ferox*, *Aspideretes singularis*, *T. [Amyda] mira*, *T. [Amyda?] tritor*); Hoffmann, 1890 (*Trionyx ?gangeticus*, high quality halftones); Loveridge and Williams, 1957 (*Trionyx triunguis**, *Cyclanorbis elegans*, *C. senegalensis**, *Cycloderma aubryi*, *C. frenatum**, these are line drawings of particularly high quality, also repeated in Wermuth and Mertens, 1961), Man-sharamani, 1965 (*Trionyx gangeticus*, figures crude, many sutures lacking); Michaux, 1973 (*Trionyx* cf. *bruxelliensis*); Moody and Walker, 1970 (*Eurycephalochelys fowleri**); Ogushi,

1911 (*Trionyx sinensis [japonicus]*, 18 high quality halftones of sectioned skulls and disarticulated elements, many showing positions of soft structures); Ogushi, 1913 (*Trionyx sinensis [japonicus]*, description of nerves, arteries, veins, and muscles in head and postcranium; figures 11, 20, and 51 are of particular use in understanding trionychid skulls); Pandya, 1951 (*Lissemys punctata*, includes sagittal view); Pope, 1935 (*Pelochelys bibroni**); Prasad, 1958 (*Chitra indica*, an incredibly bad figure in which the orbits are labeled nares and the temporal fossae are labeled orbits); Siebenrock, 1897 (*Chitra indica*, sagittal section, oblique view of ear; *Cyclanorbis senegalensis*, sagittal

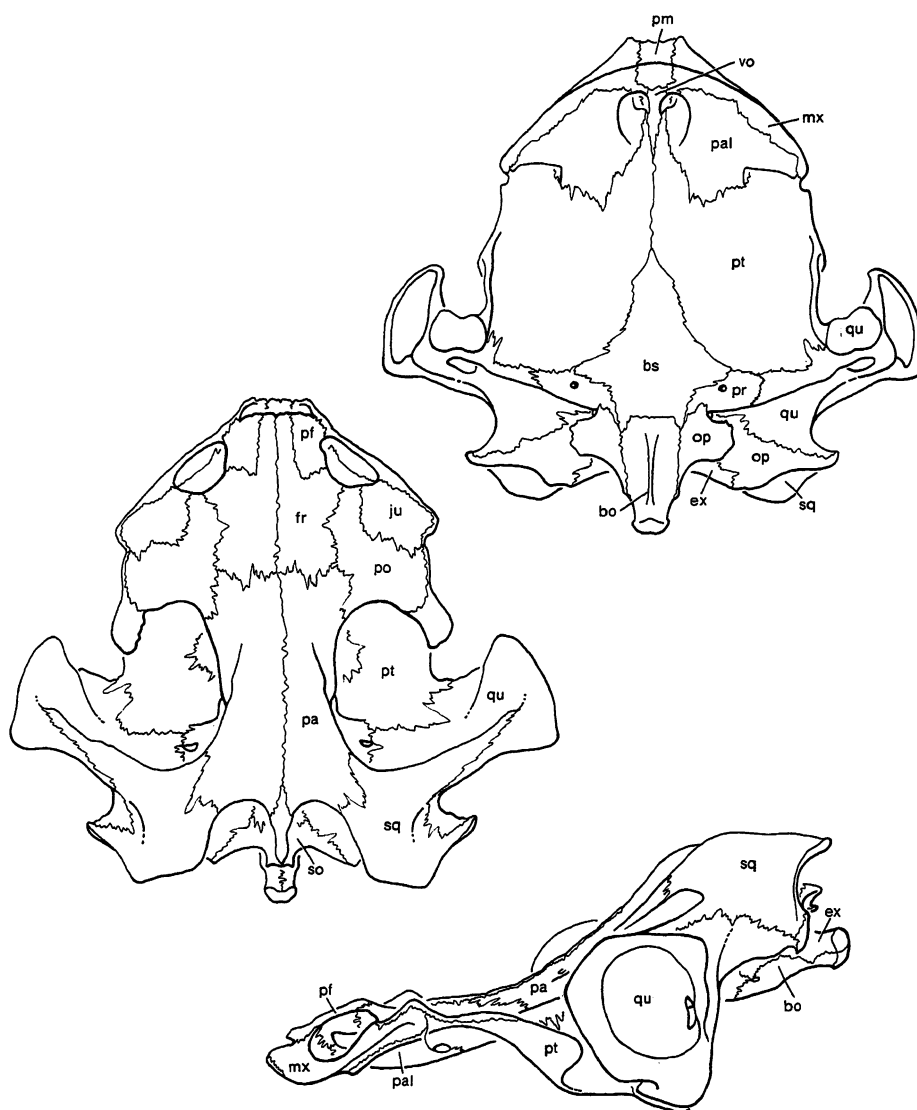


FIG. 144. *Chelus fimbriata* (AMNH 108955, 104mm.), Chelidae, no data. From Gaffney (1977a).

section, oblique view of ear; *Trionyx sinensis*, inner view of cavum labyrinthicum*; *Dogania* [*Trionyx*] *subplana*, oblique view of ear, lateral view); Smith, 1931 (*Pelochelys bibroni*, *Chitra indica*, the above are only dorsal views; *Trionyx gangeticus*, *T. hurum*, the last two are palatal views and lower jaws); Stejneger, 1944 (uses *Amyda* rather than *Trionyx*; *Trionyx spin-*

iferus, good line drawing, all the rest are photos, mostly of good quality but sutures indistinct; *T. muticus*, *T. ferox*, *T. spiniferus* [*emoryi*], *T. ferox* [*agassizii*]); Webb, 1962 (*Trionyx muticus*, *T. spiniferus*, some sutures missing); Wegner, 1959 (*Trionyx* [*Amyda*] *ferox*, good half tone of ethmoid region); Williston, 1925 ("Platypeltis" sp.).

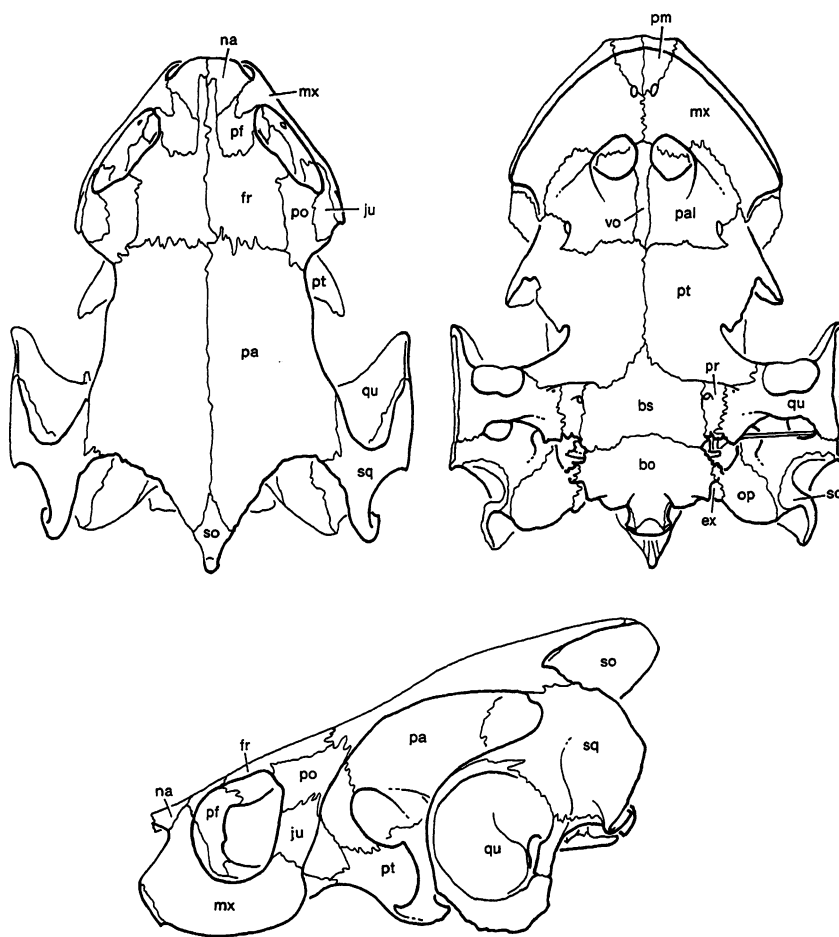


FIG. 145. *Emydura macquarrii* (AMNH 110486, 49 mm.), Chelidae, Cooper's Creek, South Australia, Australia. From Gaffney (1977a).

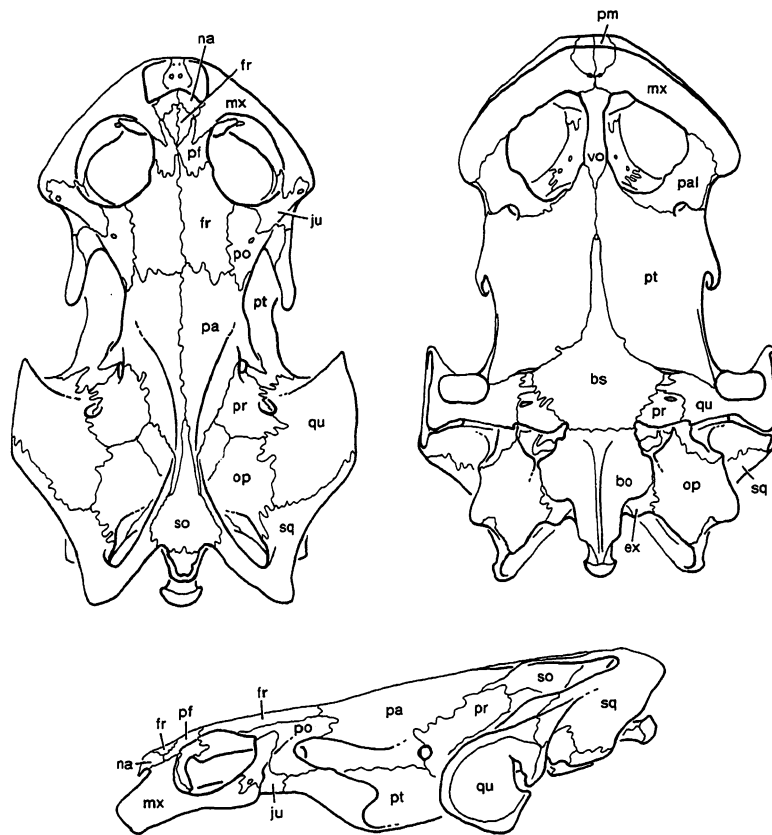


FIG. 146. *Hydromedusa tectifera* (FMNH 31032, 51 mm.), Chelidae, Itaquaguecetuba, Sao Paulo, Brazil. From Gaffney (1977a).

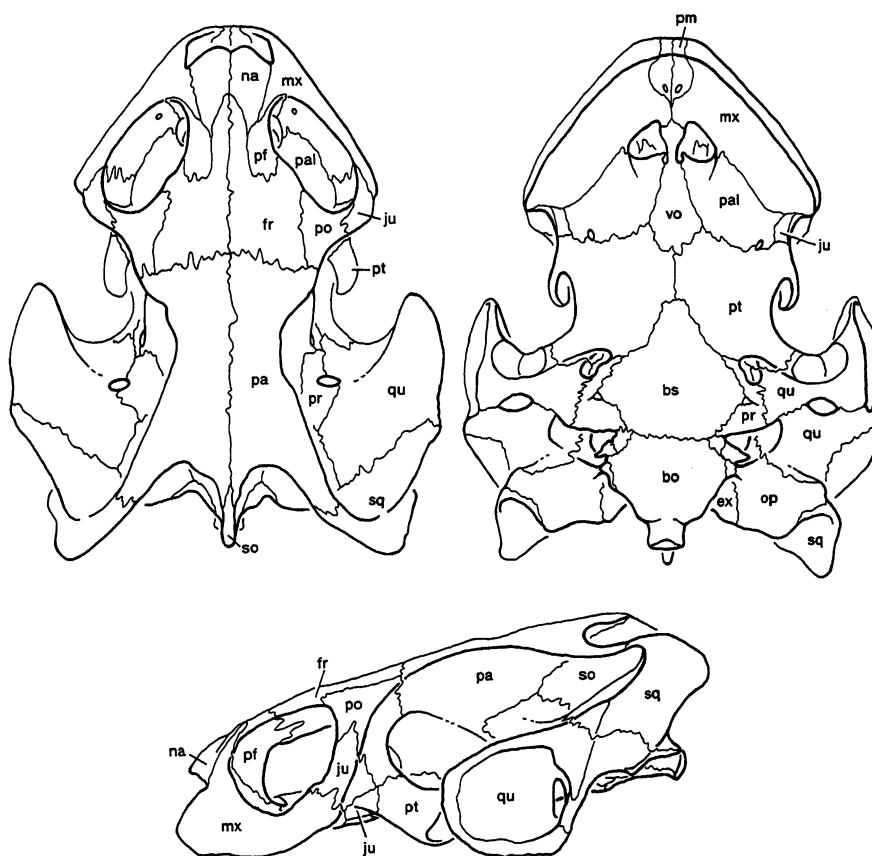


FIG. 147. *Mesoclemys gibba* (FMNH 45669, 33 mm.), Chelidae, Yarinacocha, Loreto, Peru. Referred to *Hydraspis* by Boulenger (1889) and many recent authors. From Gaffney (1977a).

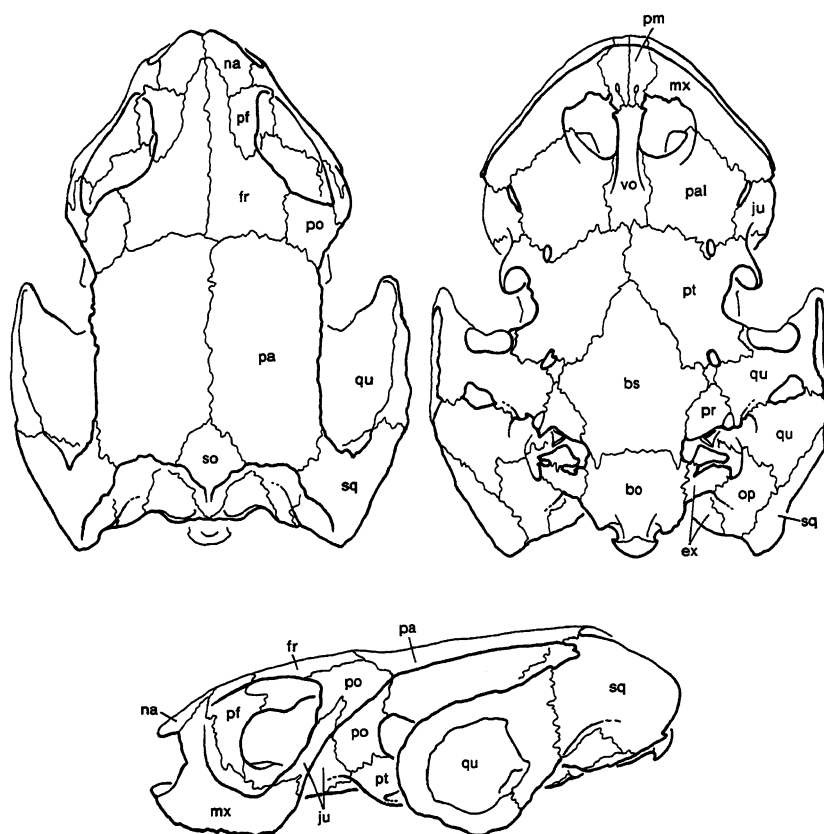


FIG. 148. *Platemys platycephala* (AMNH 74811, 28 mm.), Chelidae, no data. From Gaffney (1977a).

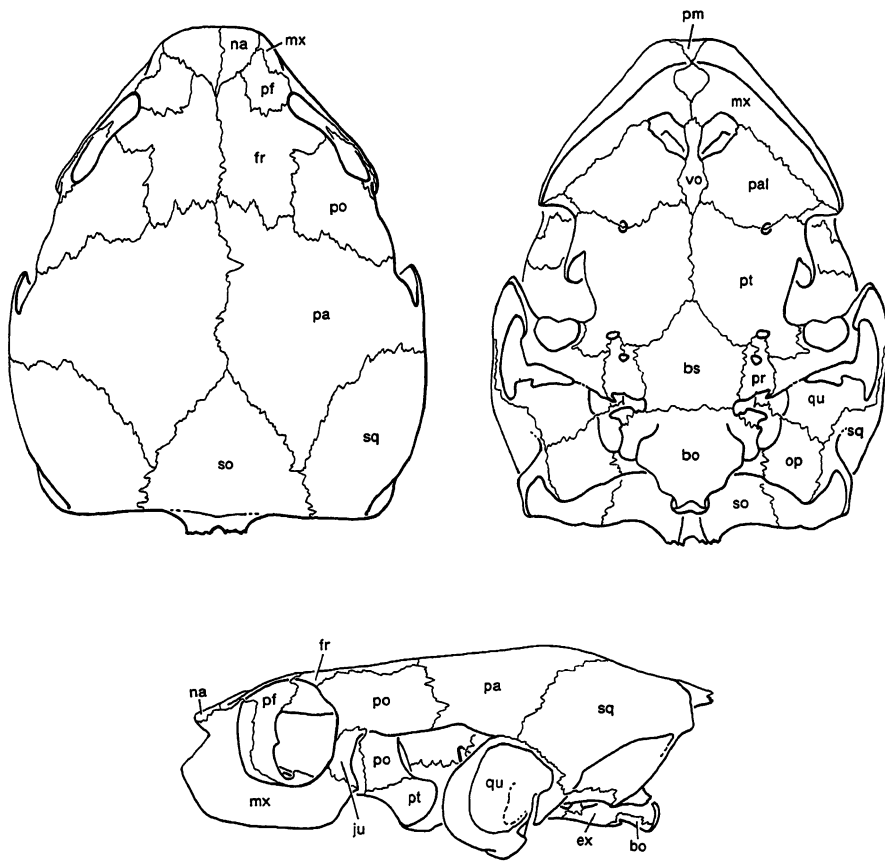


FIG. 149. *Pseudemydura umbrina* (Western Australian Museum R29341, 35 mm.), Chelidae, Twin Swamp Reserve, Western Australia. Premaxilla missing in specimen. Although there are two foramina in the vicinity of the foramen posterior canalis carotici interni, the anterior foramen is of unknown content, whereas the posterior one is for the internal carotid artery. From Gaffney (1977a).

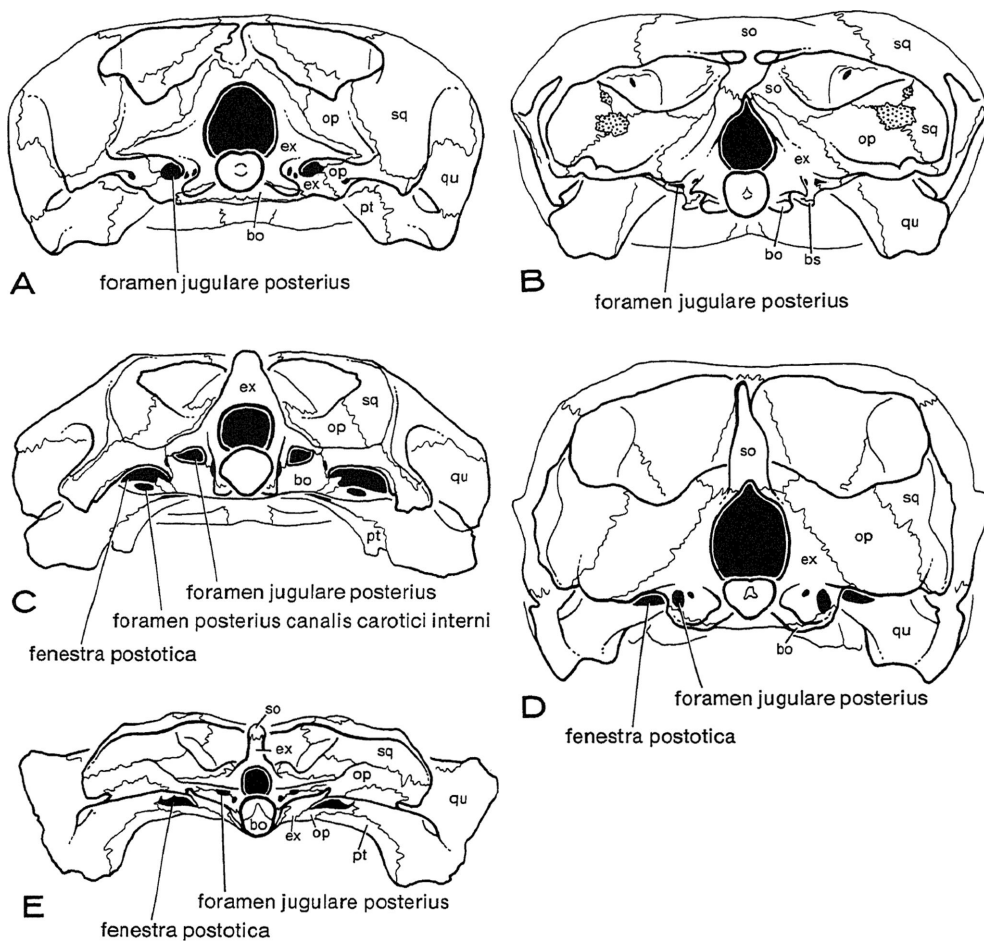


FIG. 150. Occipital views of Recent Chelidae. A. *Platemys platycephala* (AMNH 74811); B. *Pseudemys umbrina* (Western Australian Museum R 29341); C. *Hydromedusa tectifera* (NMNH 15189); D. *Emydura* sp. (AMNH 76199); E. *Chelus fimbriata* (AMNH 108955). From Gaffney (1977a).

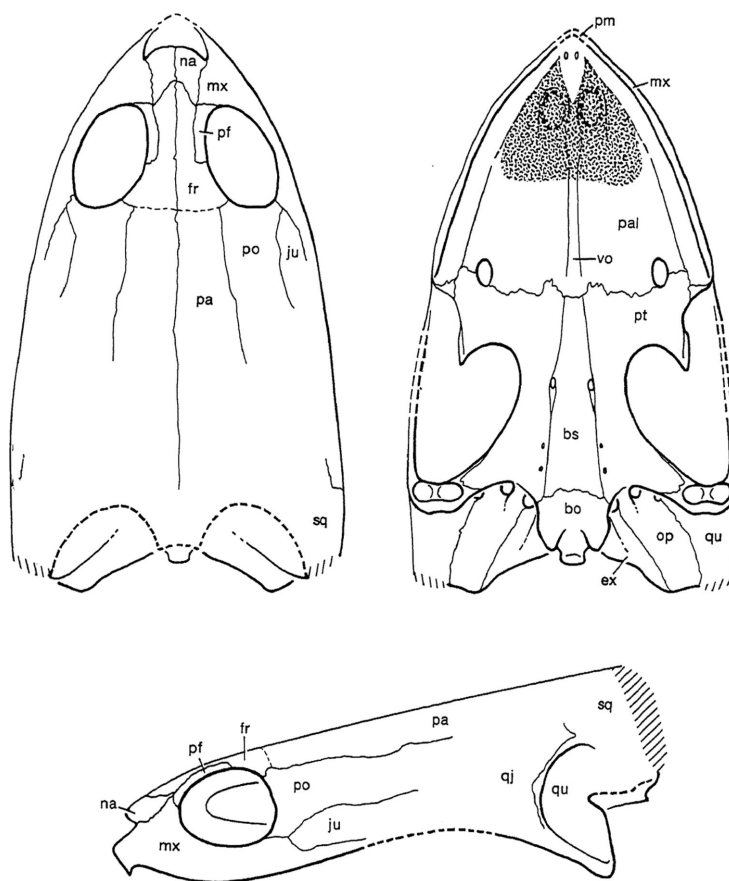


FIG. 151. *Glyptops plicatulus* (AMNH 336, 66 mm.; Bone Cabin Quarry; and YPM 1357; Marsh Quarry Nine), Glyptopsidae, Morrison Formation, late Jurassic, near Como, Wyoming.

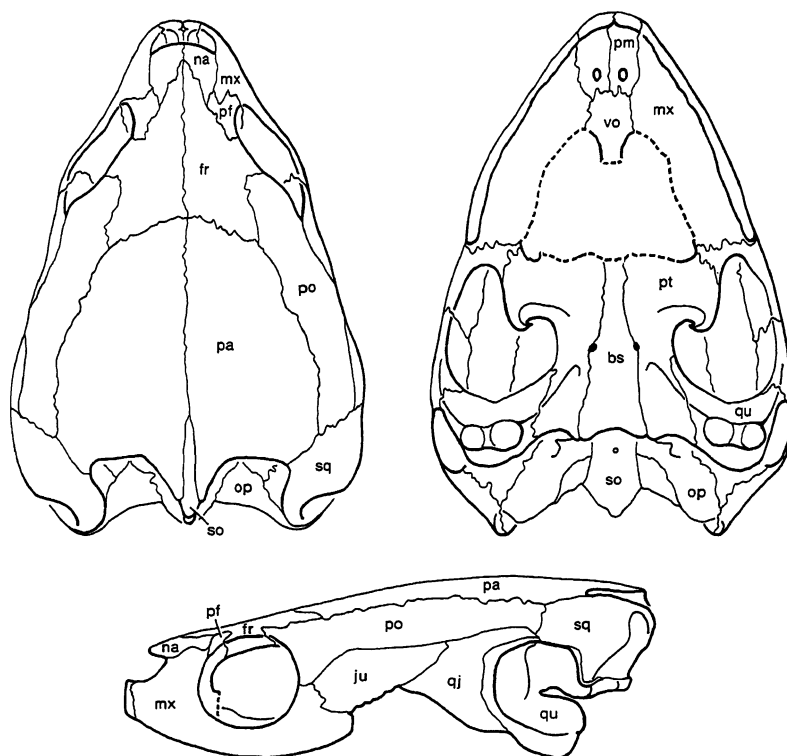


FIG. 152. *Mesochelys durlstonensis* (Cambridge University, Museum of Zoology, T 1041; 49 mm.), Glyptopsidae, Durlston Formation (?), Cretaceous, Durlston Bay, Dorset, England. After Evans and Kemp (1975), *q. v.* for description and other figures.

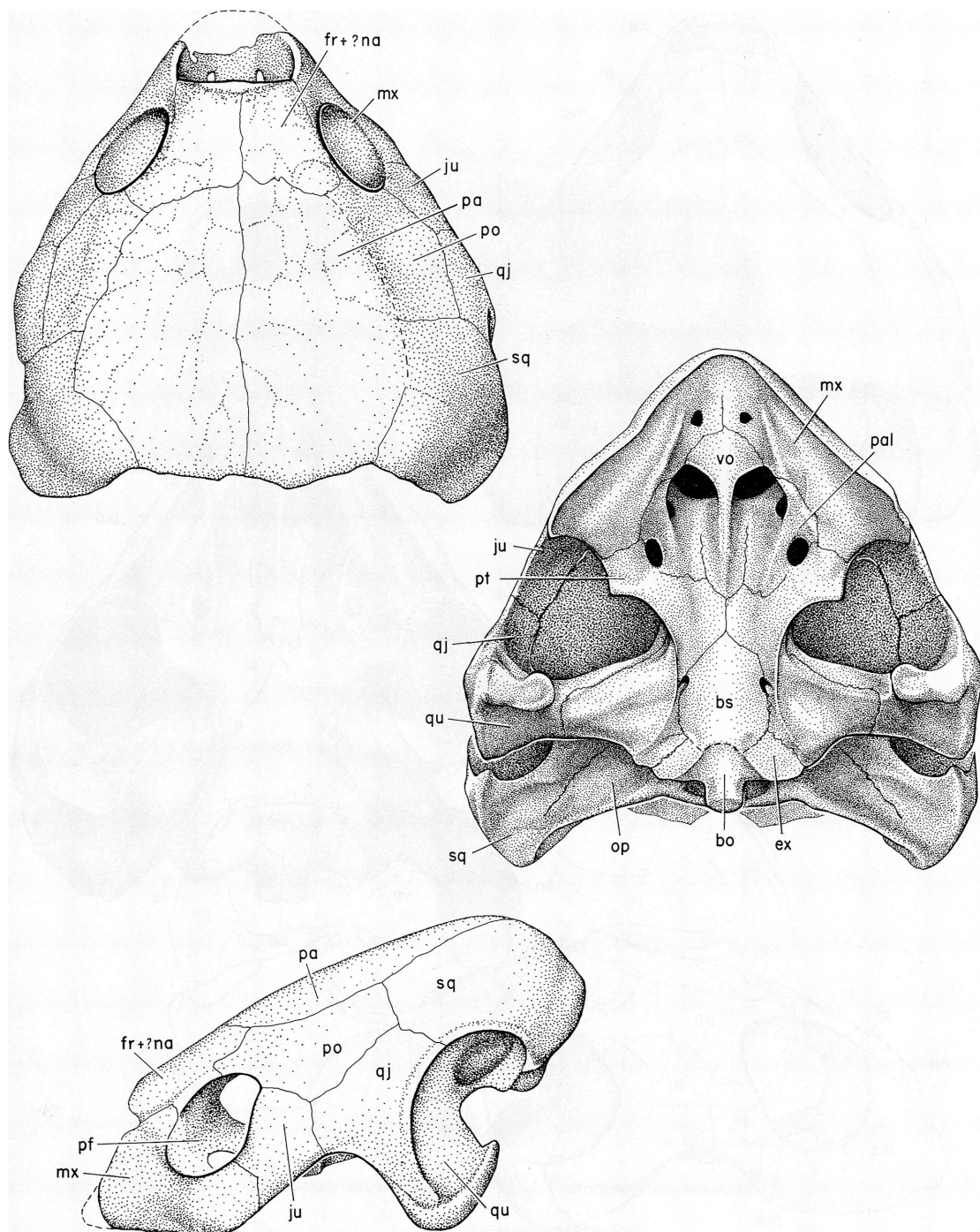


FIG. 153. *Baena arenosa* (MCZ 4072; 54 mm.), Baenidae, Willwood Formation, Eocene, near Squaw Nipple Butte, Buffalo Basin, Wyoming. Modified from Gaffney (1972a), *q. v.* for other figures.

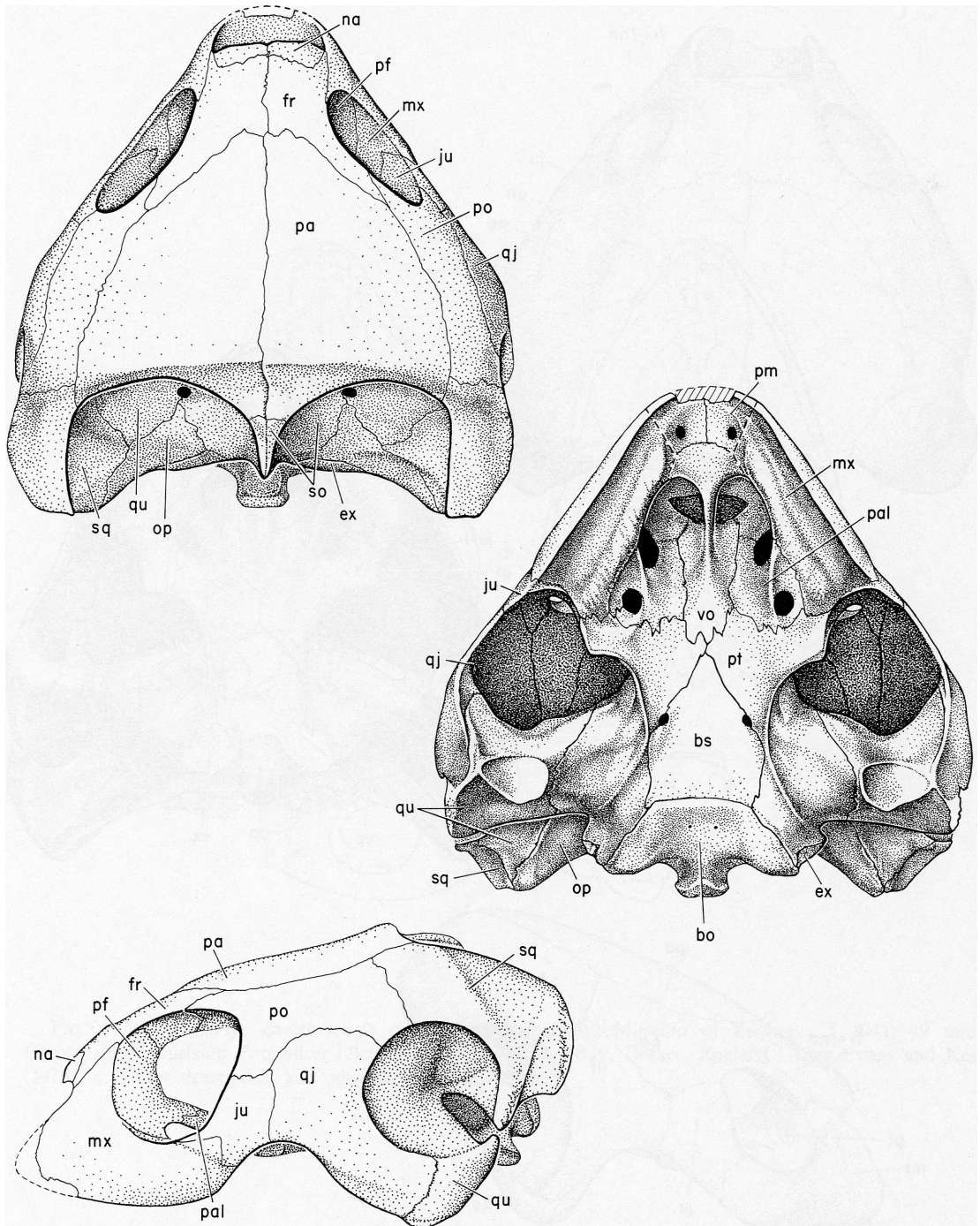


FIG. 154. *Chisternon undatum* (AMNH 5961; 68 mm.), Baenidae, Bridger Formation, Eocene, Grizzly Buttes West, Bridger Basin, Wyoming. Modified from Gaffney (1972a), *q. v.* for other figures.

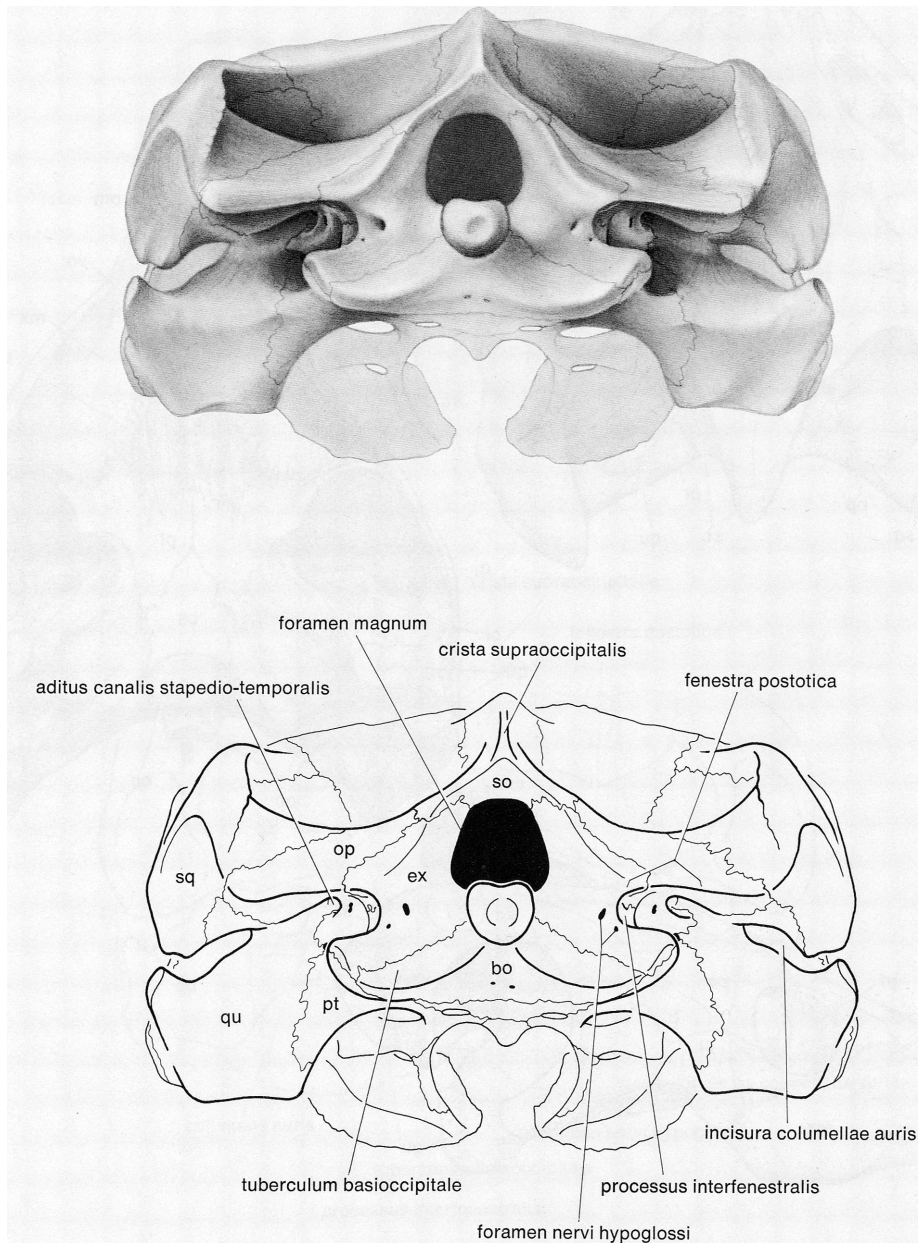


FIG. 155. *Chisternon undatum*, same data as figure 154. Occiput.

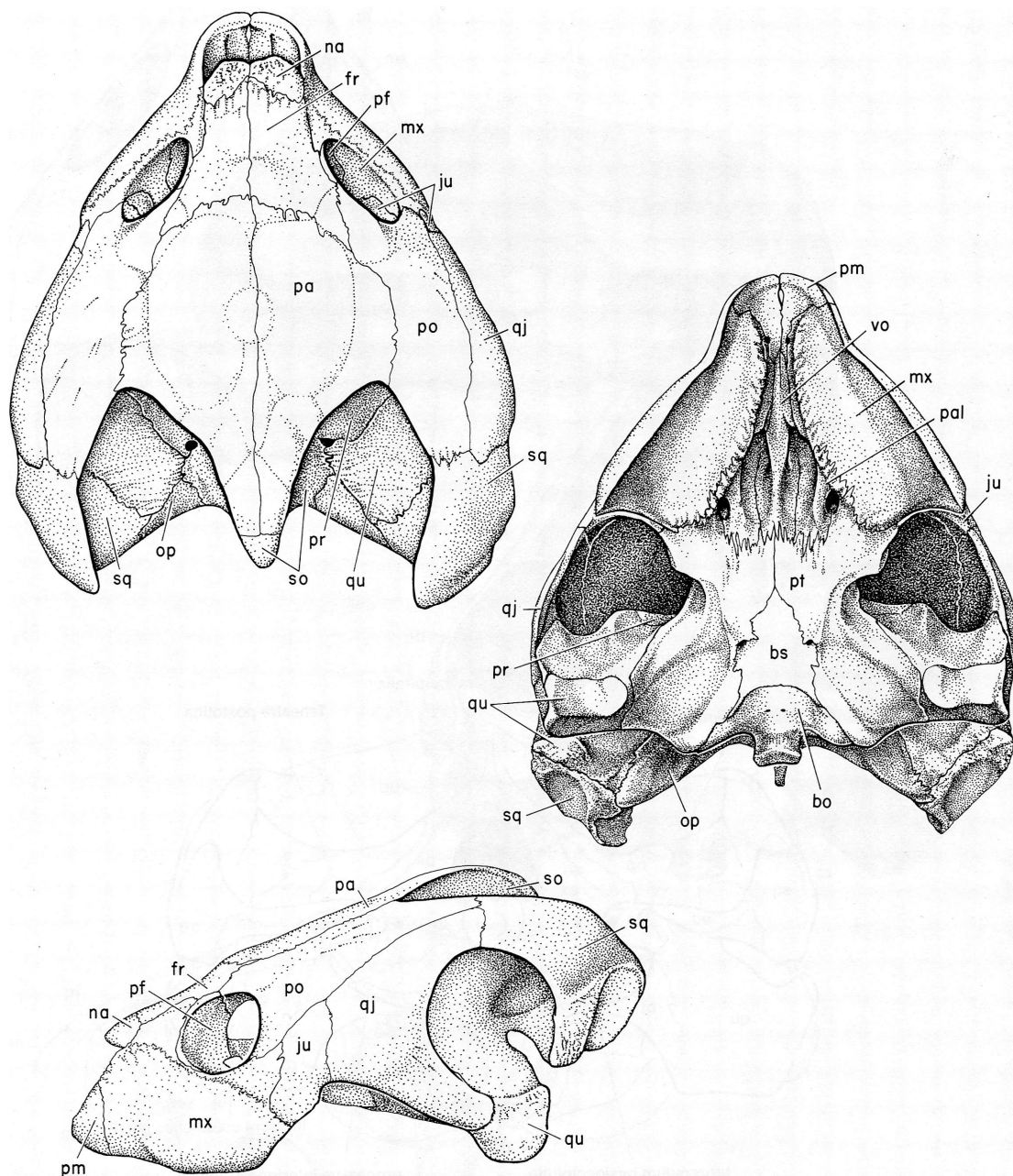


FIG. 156. *Eubaena cephalica* (YPM 1785; 66 mm.), Baenidae, Lance Formation, Late Cretaceous, Niobrara County, Wyoming. Modified from Gaffney (1972a), *q. v.* for other figures.

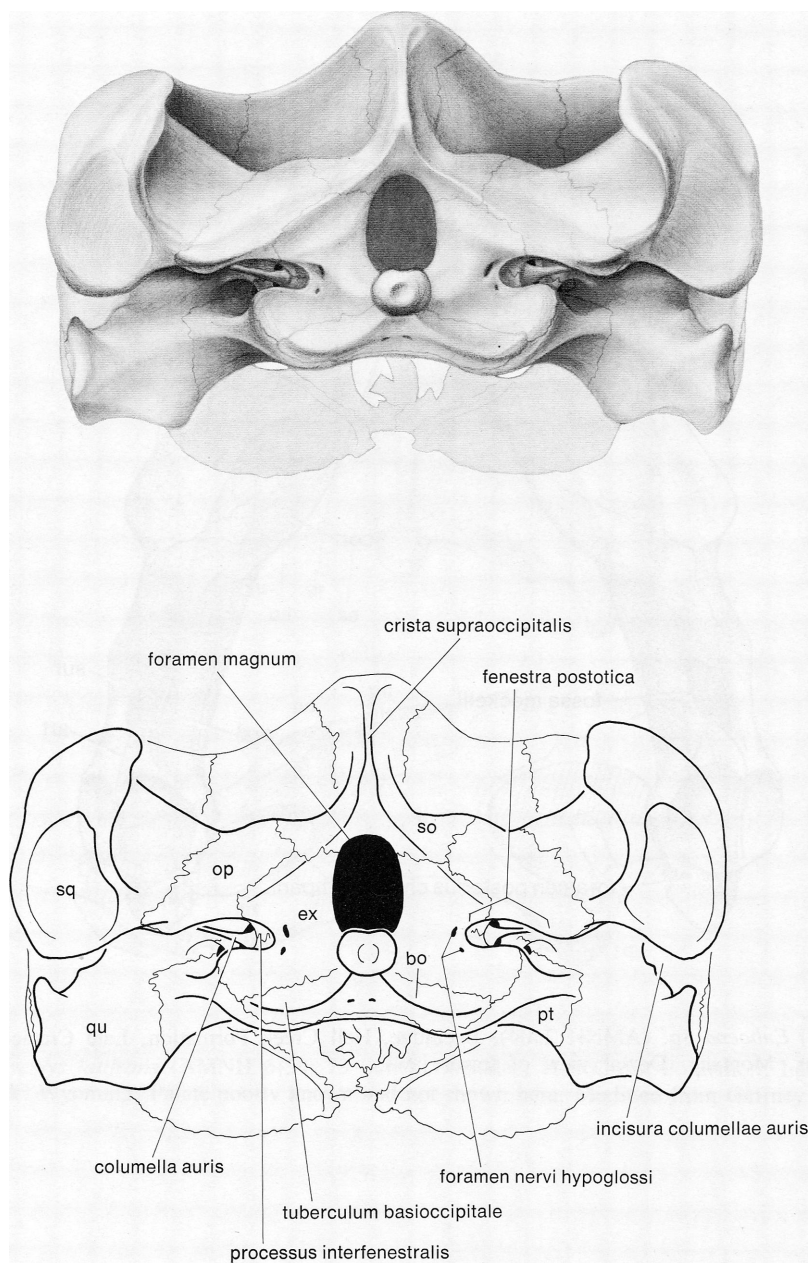


FIG. 157. *Eubaena cephalica*, same data as figure 156. Occiput.

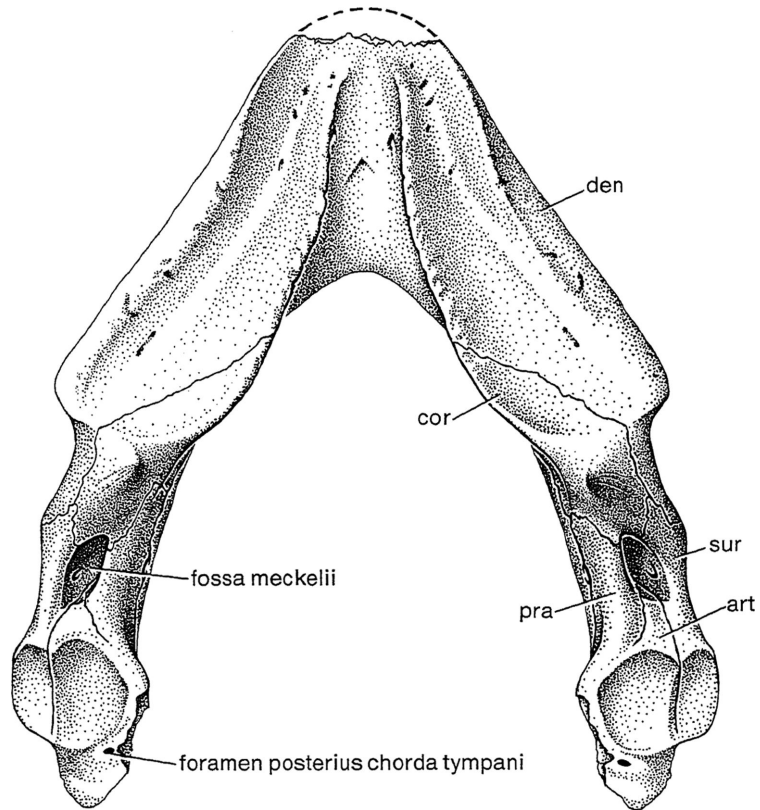


FIG. 158. (?) *Eubaena* sp. (AMNH 2604), Baenidae, Hell Creek Formation, Late Cretaceous, 26 miles south of Lismas, Montana. Dorsal view of lower jaws.

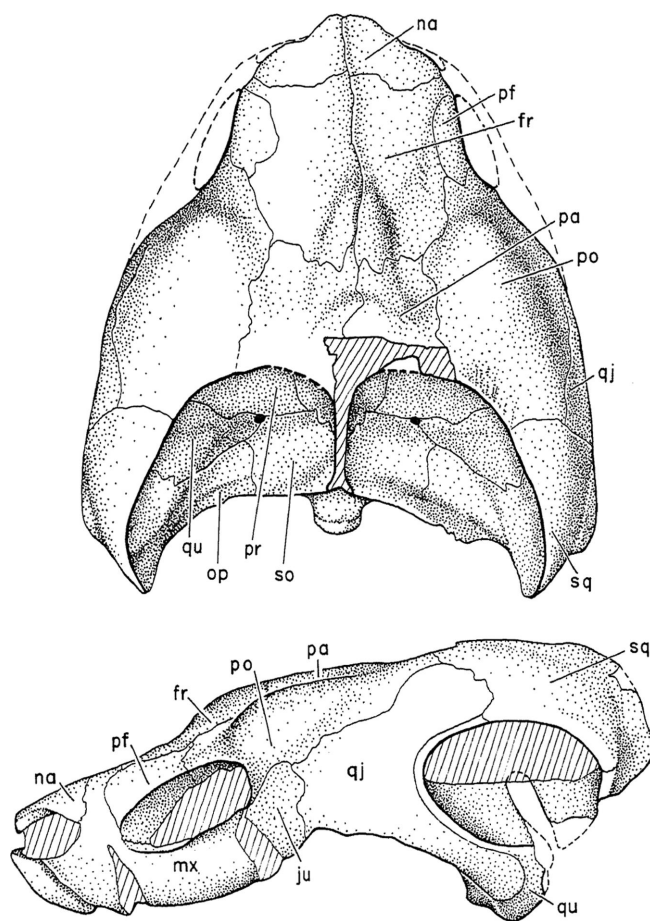


FIG. 159. *Hayemys latifrons* (AMNH 6139; 73 mm.), Baenidae, Hell Creek Formation, Late Cretaceous, Seven Mile Creek, Wyoming. Palate poorly known and not shown here. Modified from Gaffney (1972a), q. v. for other figures.

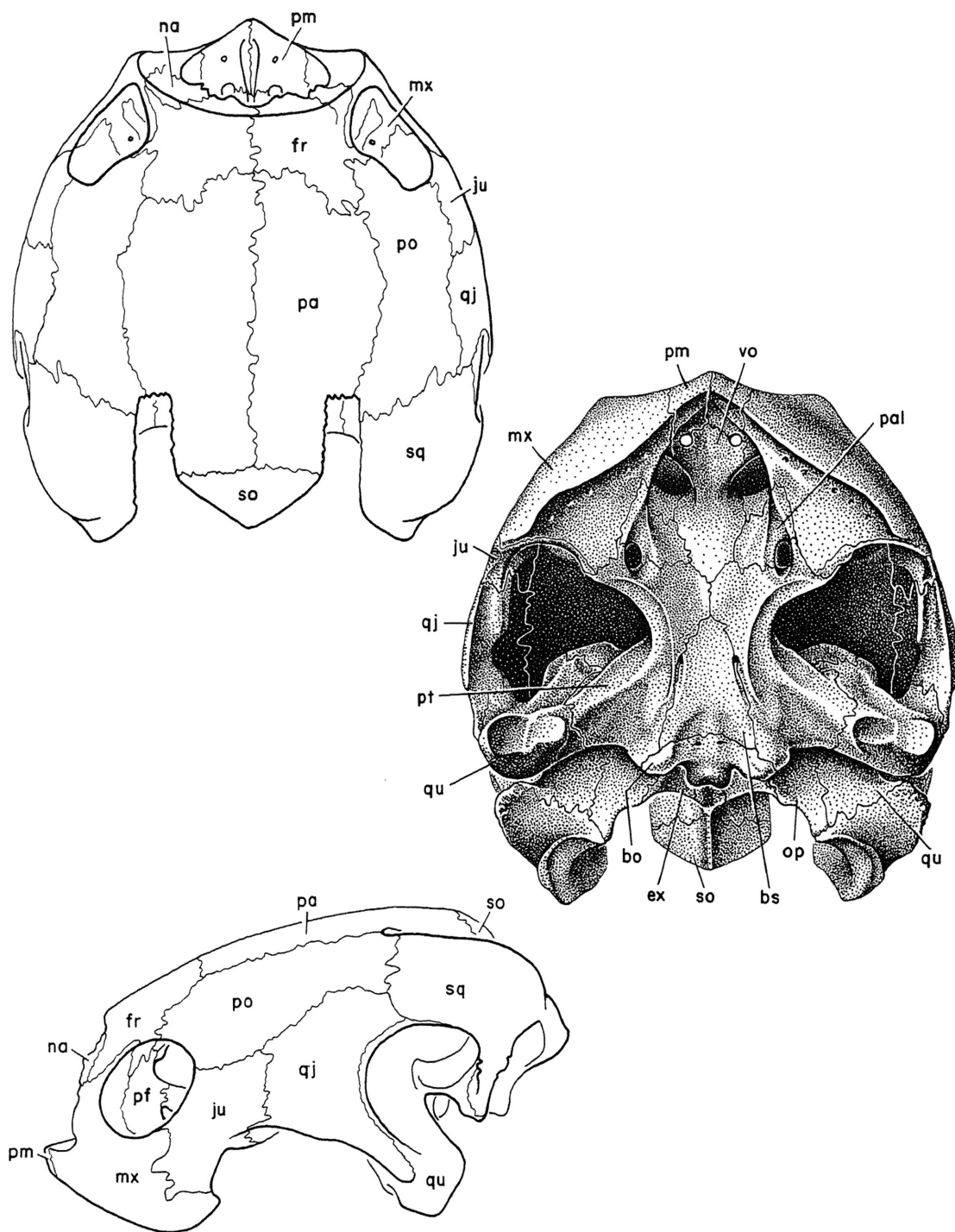


FIG. 160. *Palatobaena* sp. (Carter County Museum no. 77-11; 48 mm.), Baenidae, Medicine Rocks Formation, Paleocene, Ekalaka, Montana. I am indebted to Mr. Marshall Lambert, the collector of this skull, for lending it to me.

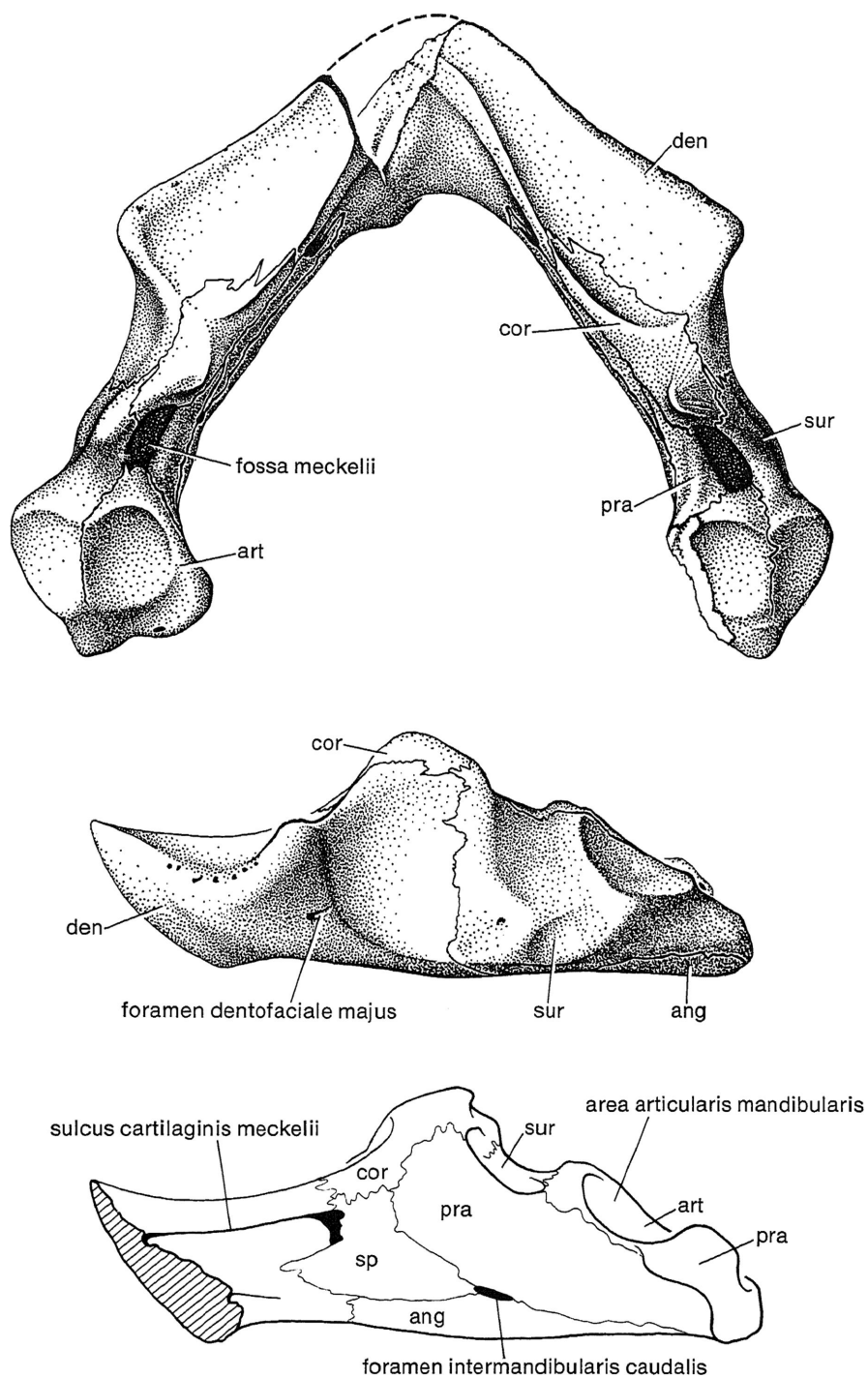


FIG. 161. (?) *Palatobaena* sp (AMNH 8277), Baenidae, Hell Creek Formation, Late Cretaceous, Bug Creek Anthills, McCone County, Montana. Upper, dorsal view of lower jaws; middle, lateral view of left ramus; bottom, medial view of right ramus. Note partially healed fracture near symphysis.

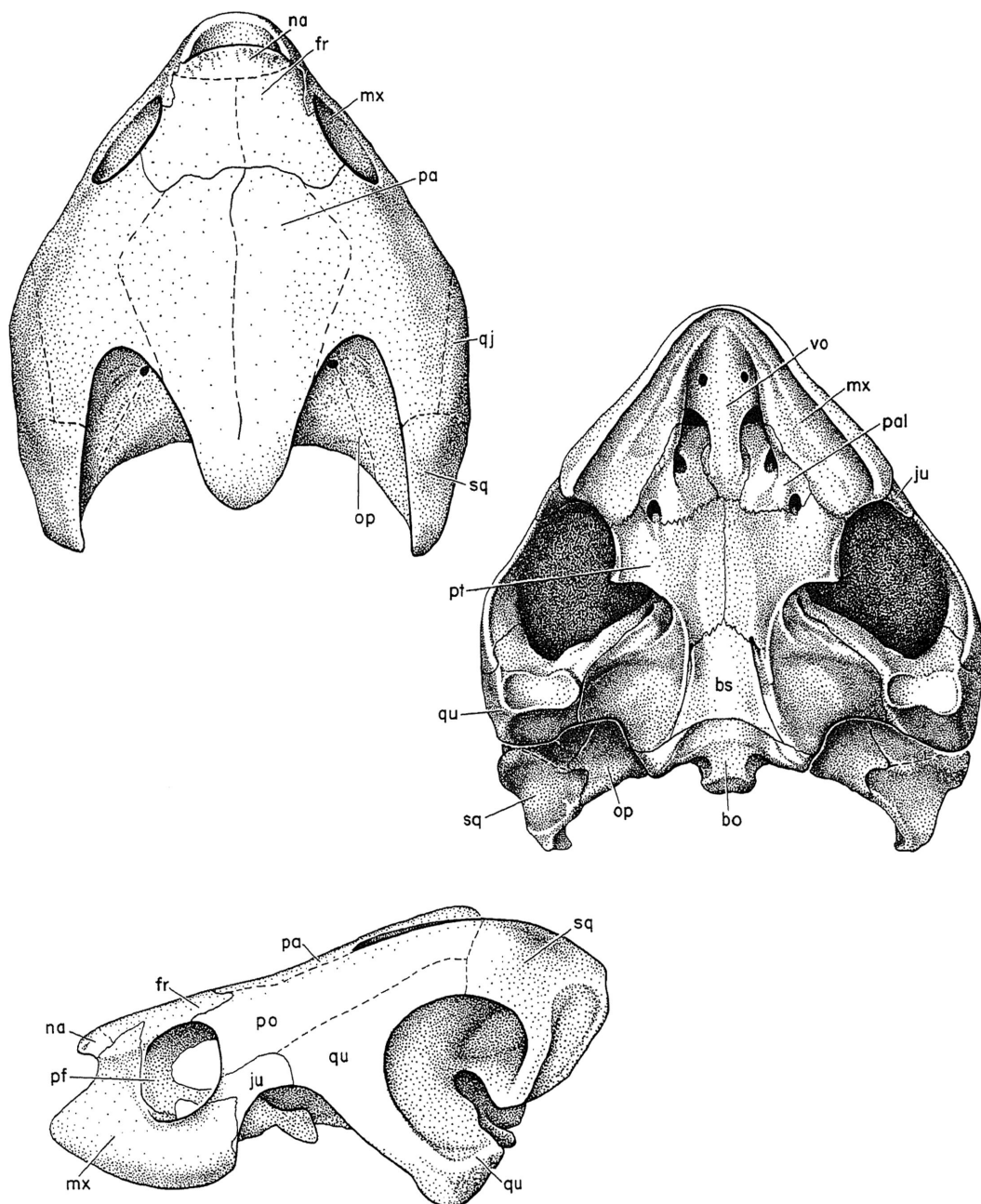


FIG. 162. *Plesiobaena antiqua* (UCMP 49759; 63 mm.), Baenidae, Lance Formation, Late Cretaceous, V-5620 near Lusk, Wyoming. Modified from Gaffney (1972a), *q. v.* for other figures.

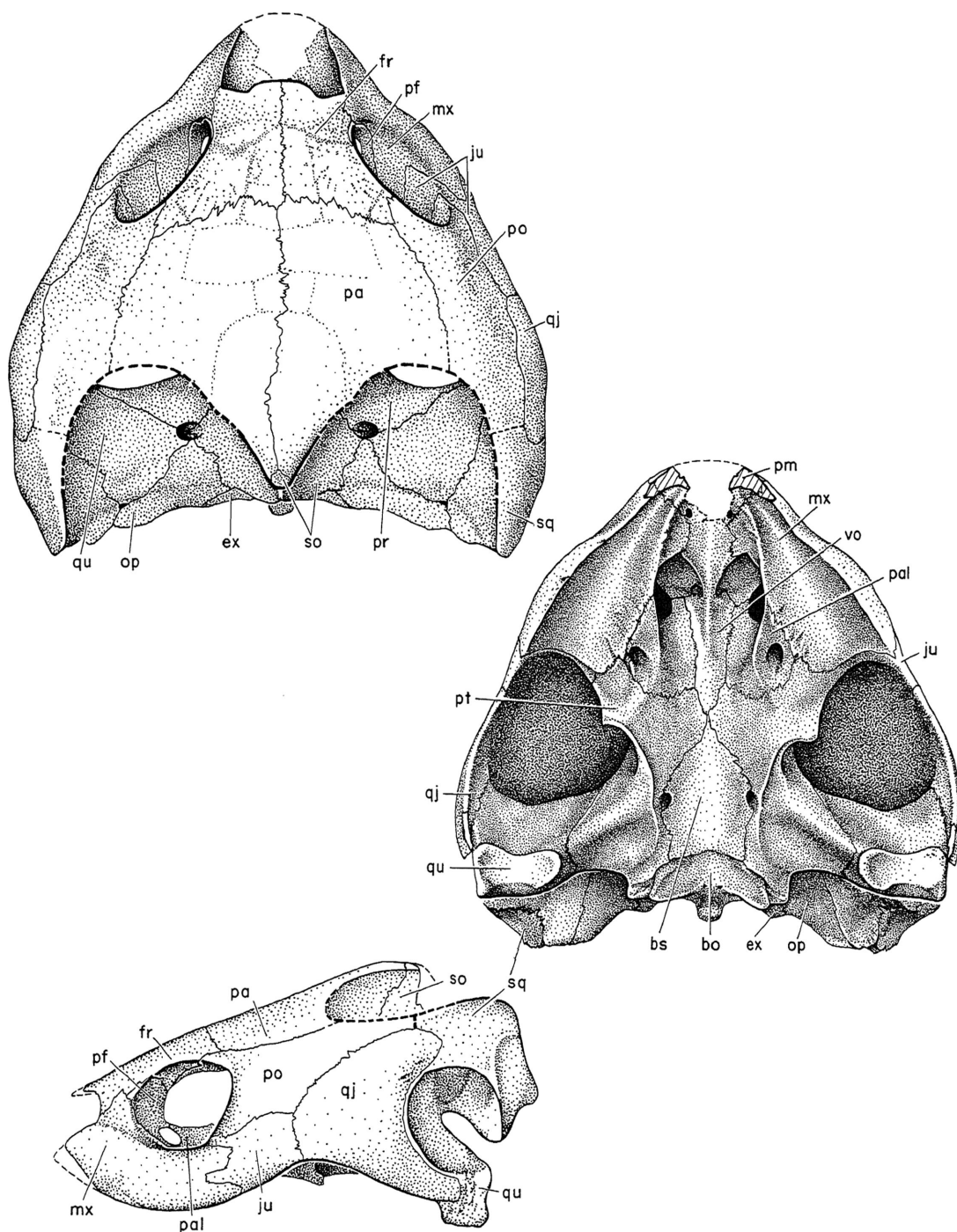


FIG. 163. *Stygiochelys estesi* (AMNH 2601; 63 mm.), Baenidae, Hell Creek Formation, Late Cretaceous, Glendive, Montana. Modified from Gaffney (1972a), *q. v.* for other figures.

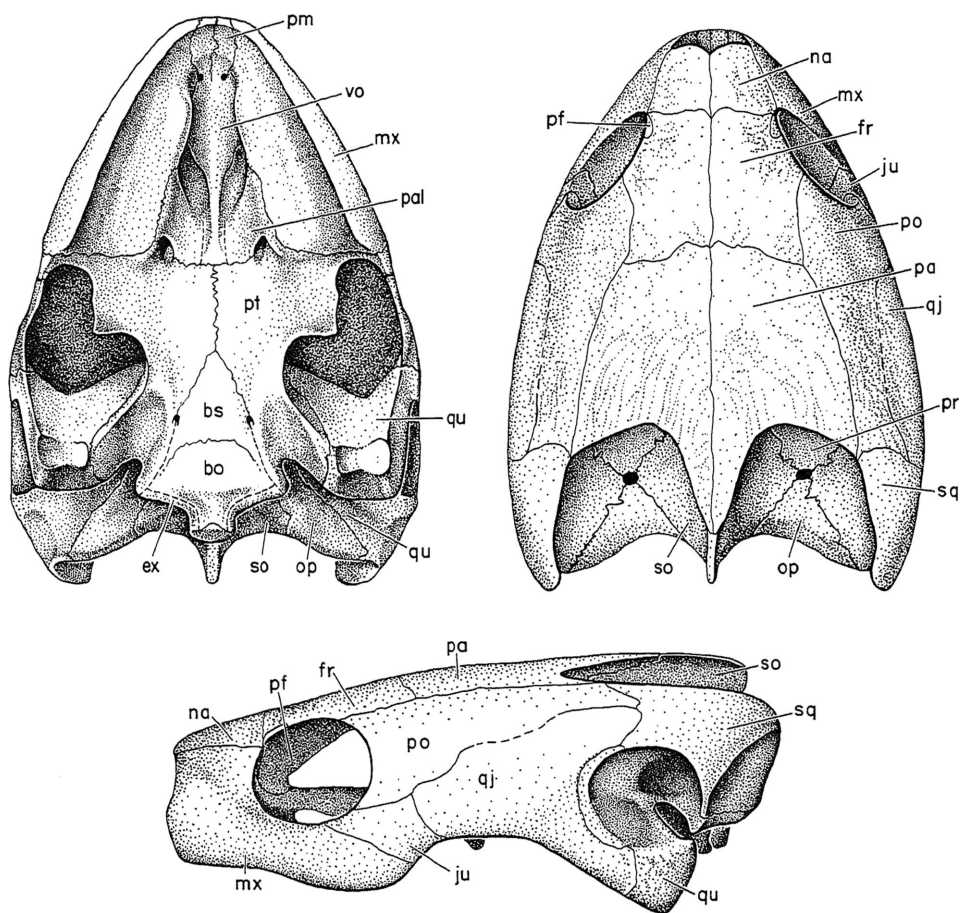


FIG. 164. *Trinitichelys hiatti* (MCZ 4070; 55 mm.), Baenidae, Trinity Sand, Early Cretaceous, Hardee, Montague County, Texas. New palatal reconstruction, rest from Gaffney (1972a), *q. v.* for other figures.

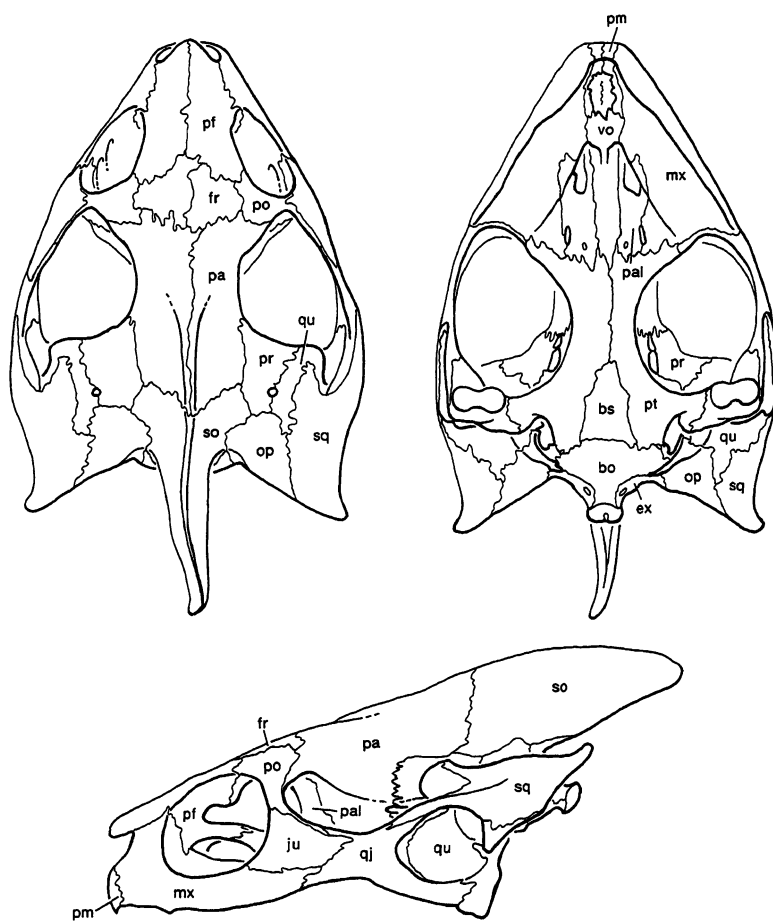


FIG. 165. *Claudius angustatus* (AMNH 65865; 39 mm.), Kinosternidae, Gainesville, Alachua County, Florida.

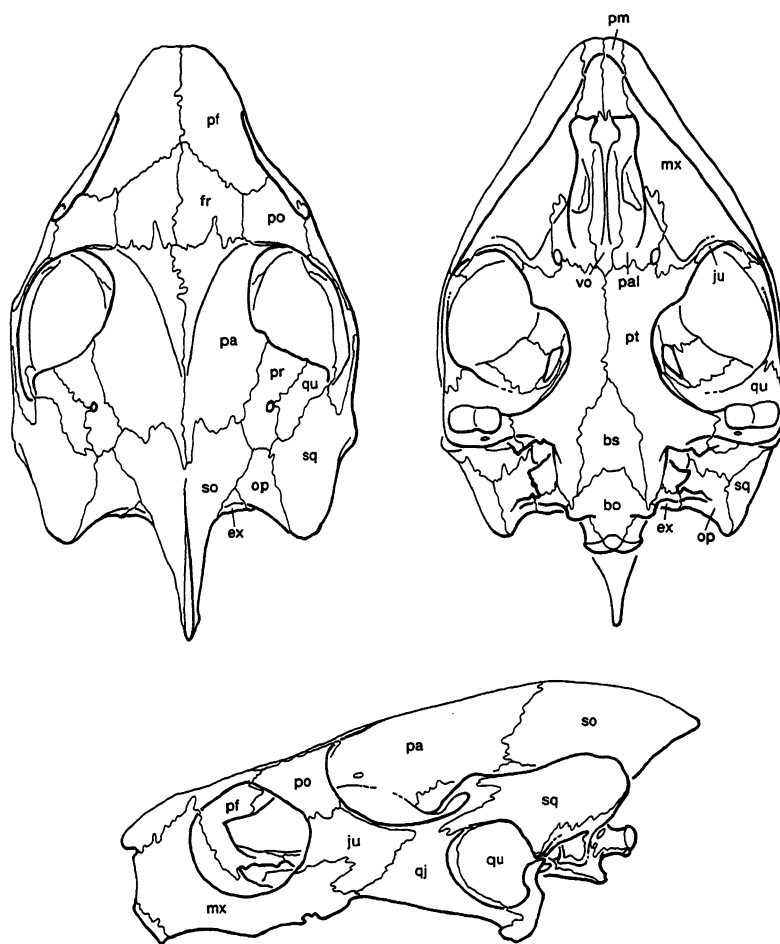


FIG. 166. *Kinosternon subrubrum* (AMNH 73825; 26 mm.), Kinosternidae, Gainesville, Alachua County, Florida.

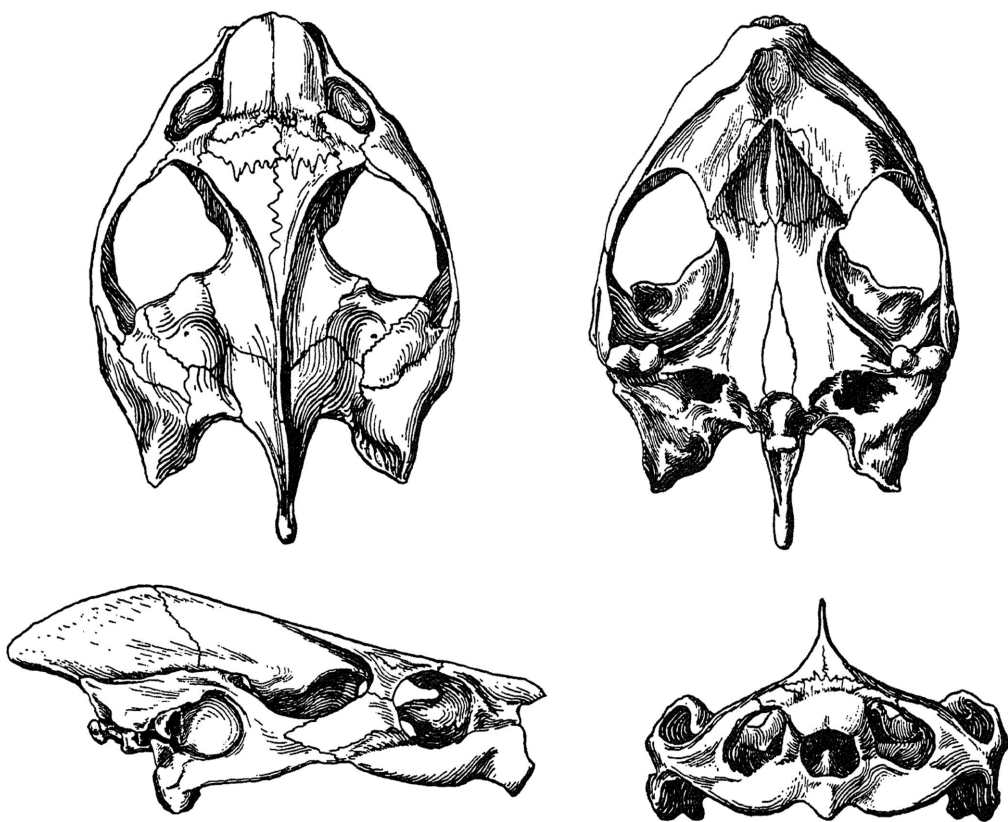


FIG. 167. *Staurotypus salvinii* (MCZ 4989; about $\times 1\frac{1}{4}$), Kinosternidae, Tehuantepec, Mexico. From Williams (1952b).

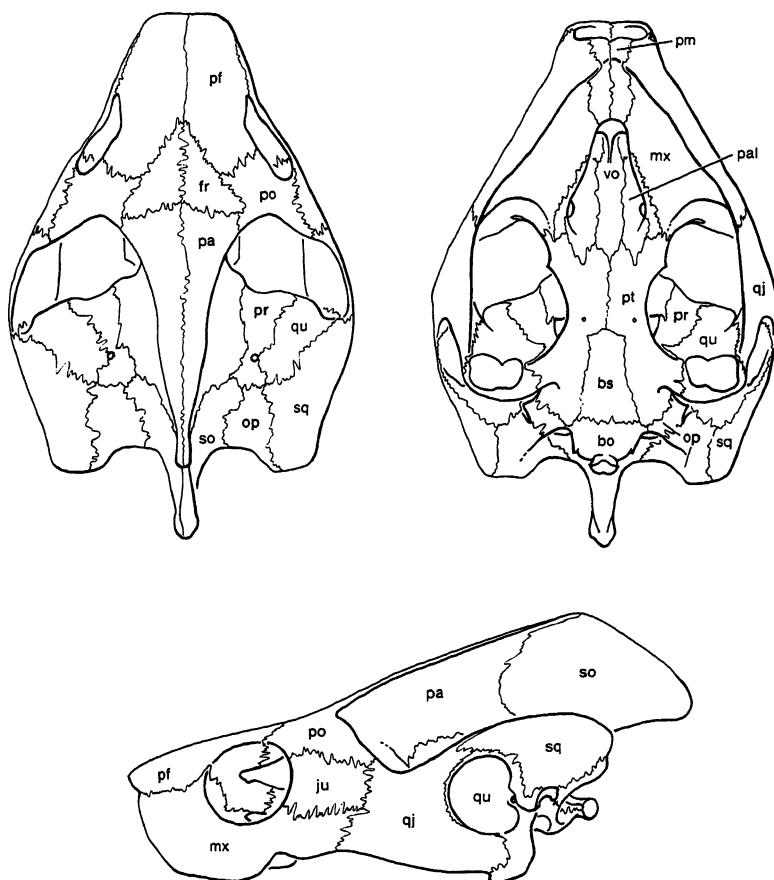


FIG. 168. *Sternotherus odoratus* (AMNH 69752; 36 mm.), Kinosternidae, Cotuit, Barnstable County, Massachusetts.

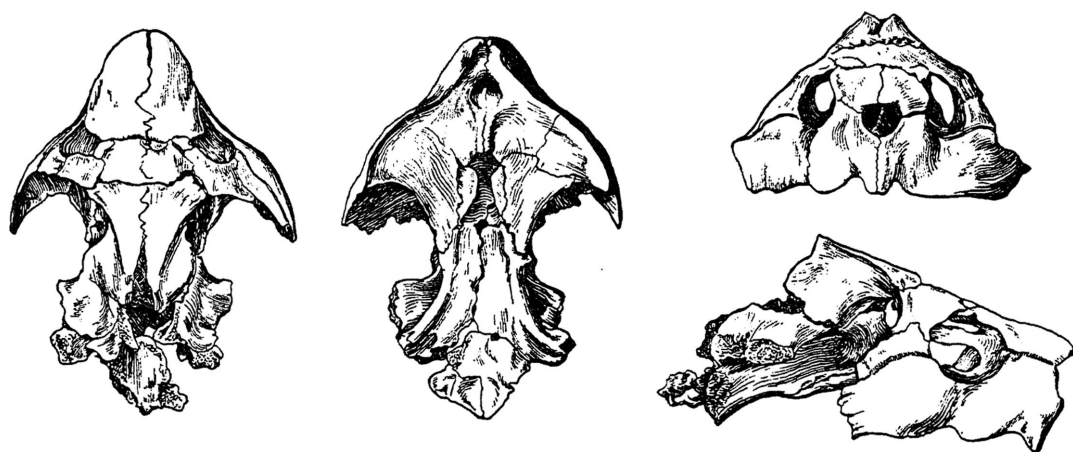


FIG. 169. *Xenochelys formosa* (PU 13686; about natural size), Kinosternidae, Chadron Formation, Oligocene, north-east of Huttenmacher Table, Indian Creek drainage, Big Badlands, South Dakota. From Williams (1952b).

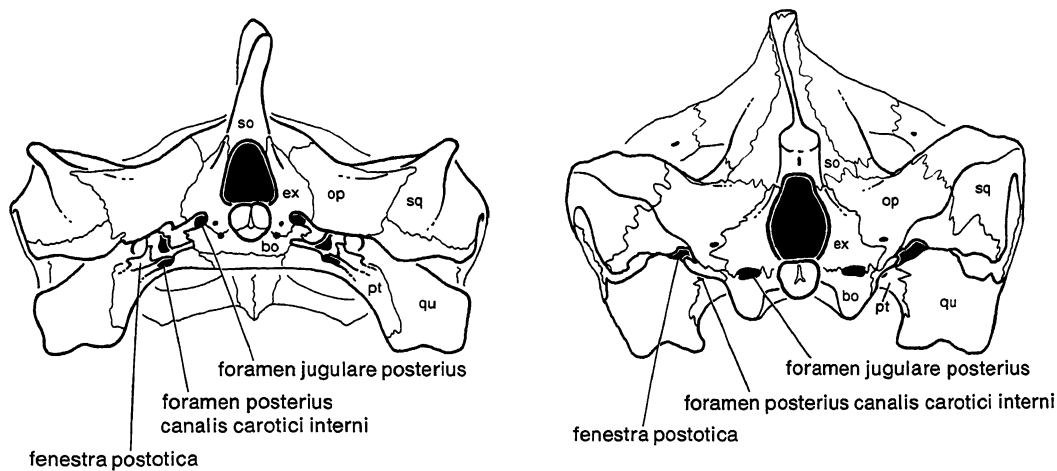


FIG. 170. Occipital views of Recent Kinostemidae. Left, *Claudius angustatus* (AMNH 65865); right, *Sternotherus odoratus* (AMNH 69752).

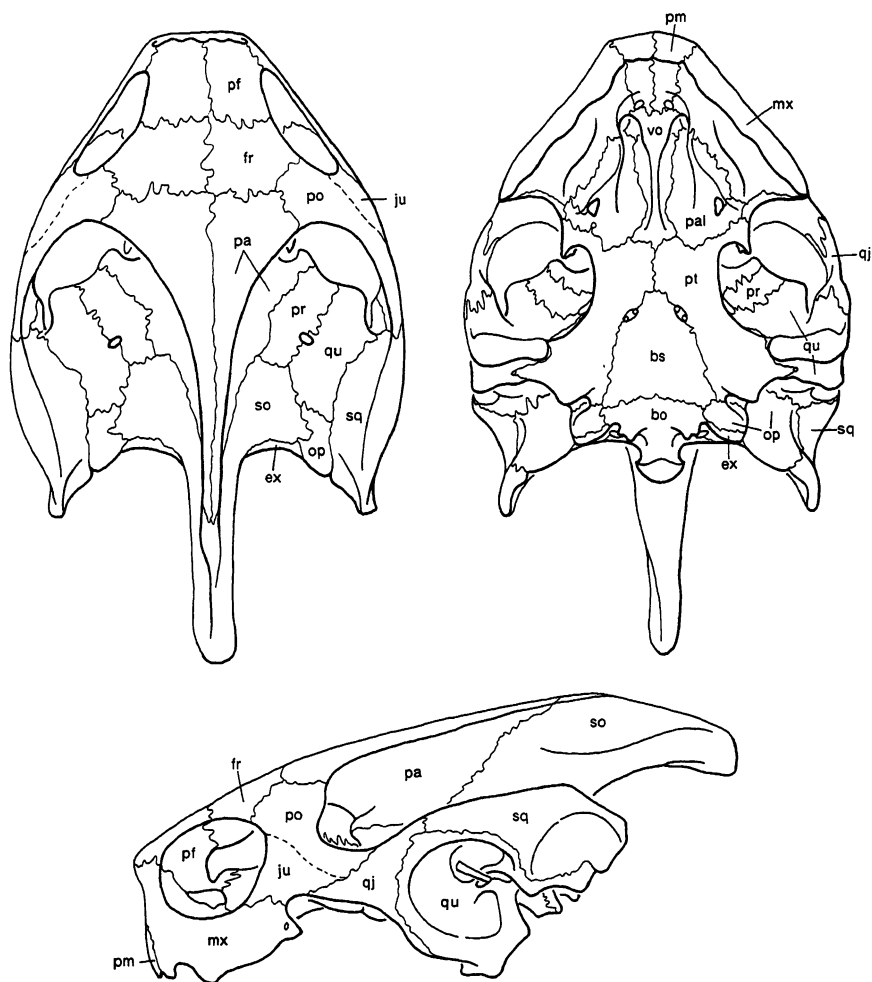


FIG. 171. *Adocus* sp. (Carter County Museum no. 60-15, 67 mm.), Dermatemydidae, Hell Creek Formation, late Cretaceous, Fallon County, Montana.

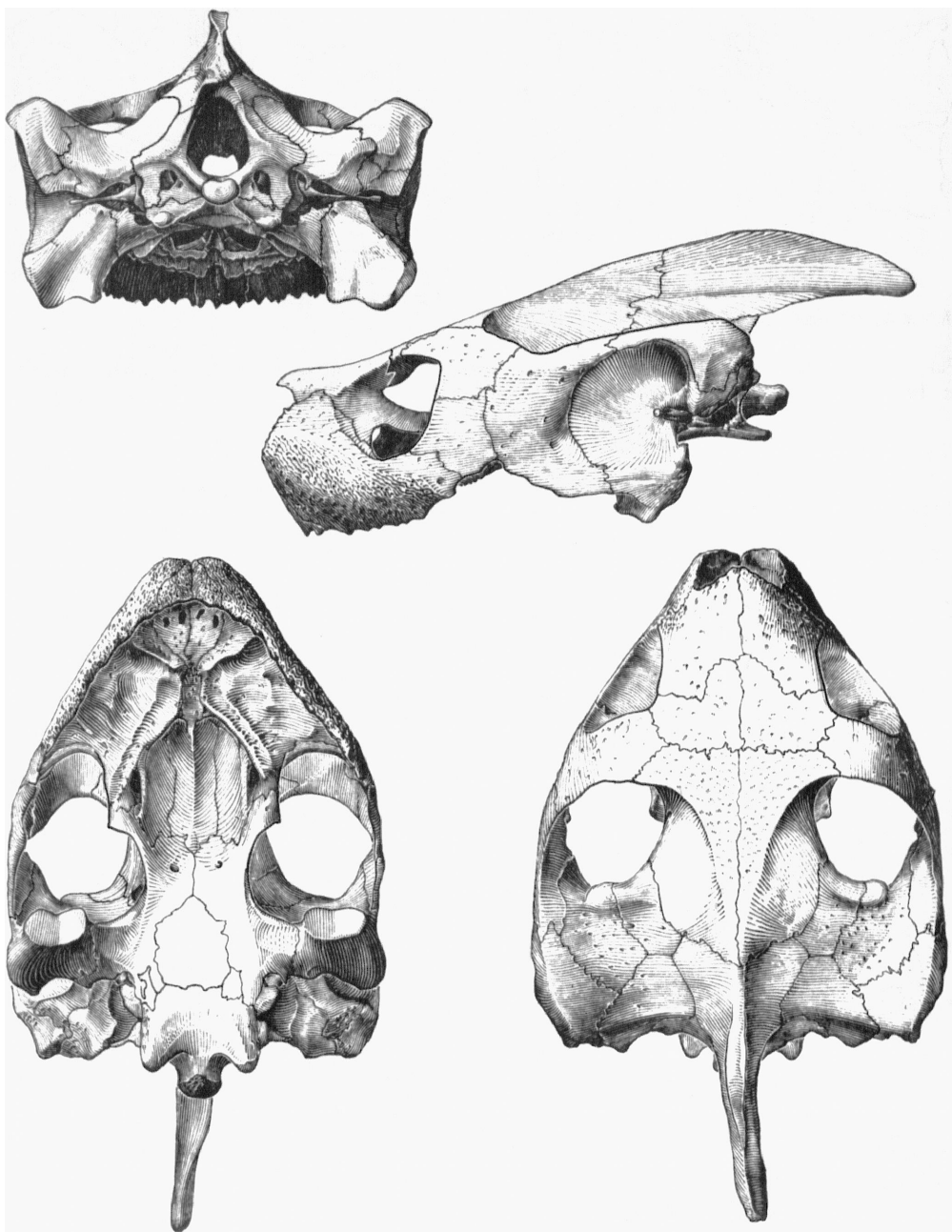


FIG. 172. *Dermatemys mawii*, Dermatemydidae. Modified from McDowell (1964).

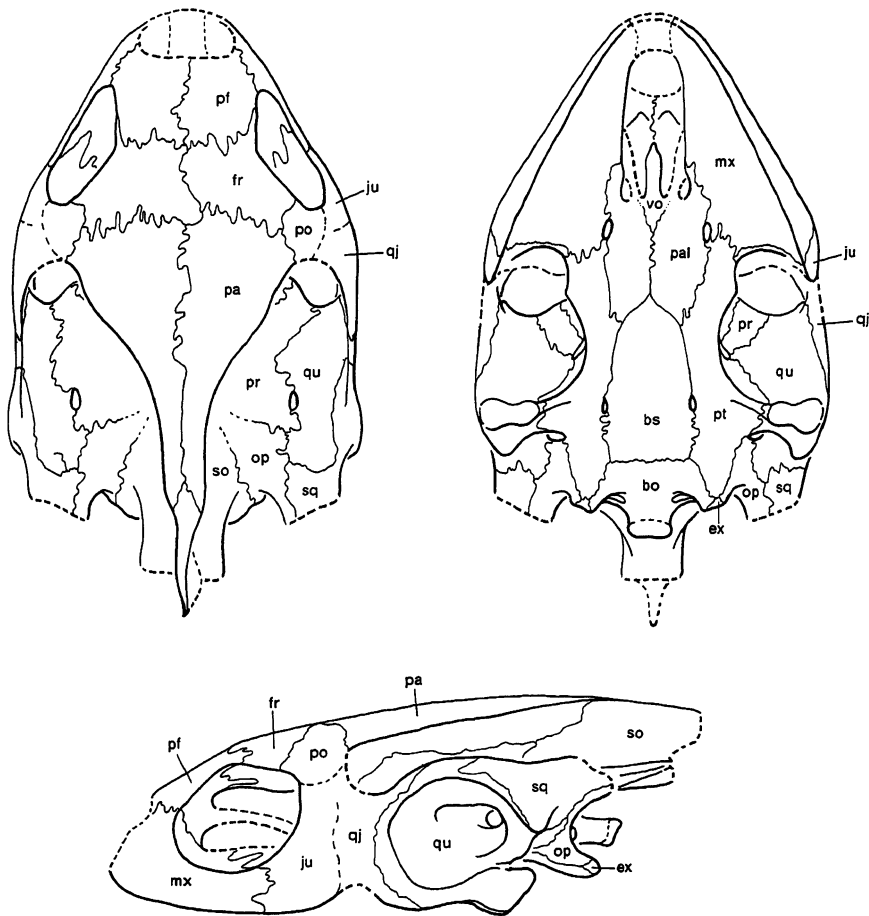


FIG. 173. Possibly *Anosteira* or *Pseudanosteira* (FMNH PR 966; 32 mm.), Carettochelyidae, Upper Eocene, Turtle Butte, Washakie Basin, Wyoming. Reconstruction based on a crushed specimen.

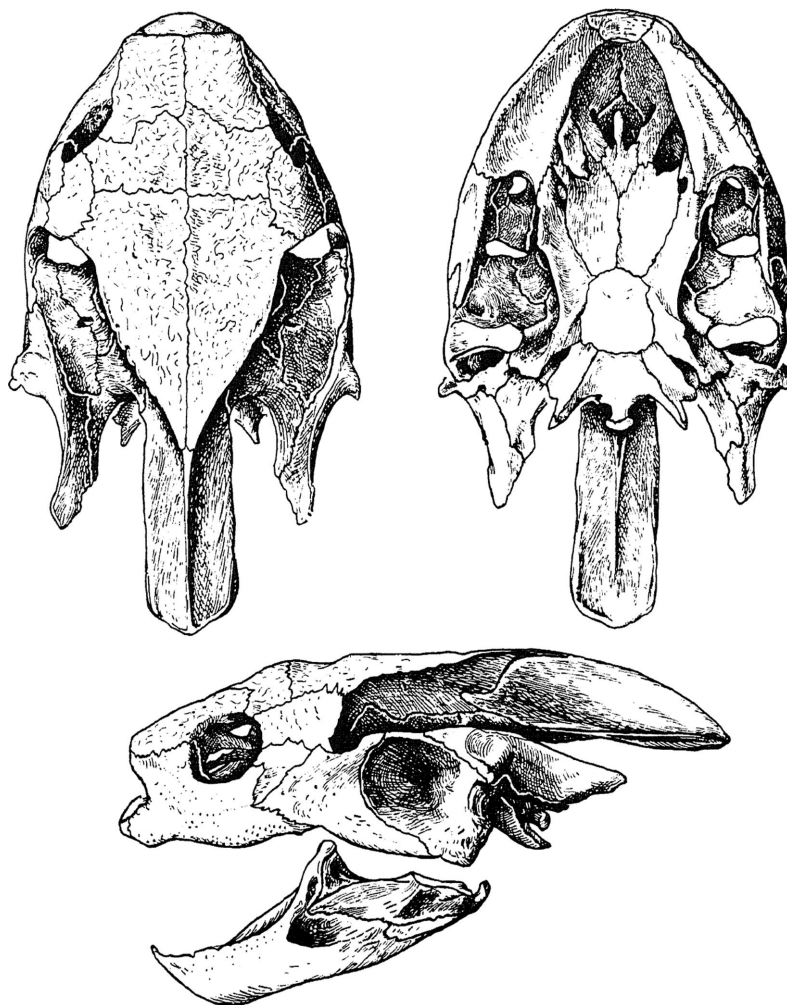


FIG. 174. *Carettochelys insculpta*, Carettochelyidae. Modified from Walther (1922), with the addition of sutures from AMNH 84212 (Fly River, Papua).

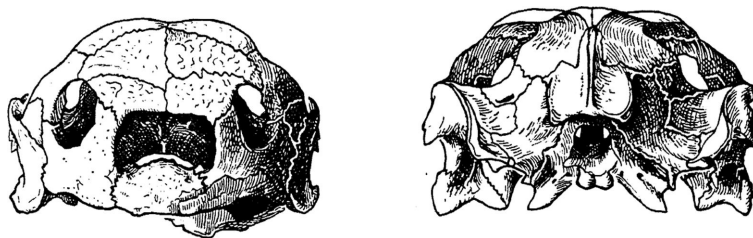


FIG. 175. *Carettochelys insculpta*, Carettochelyidae. Modified from Walther (1922), with the addition of sutures from AMNH 84212 (Fly River, Papua).

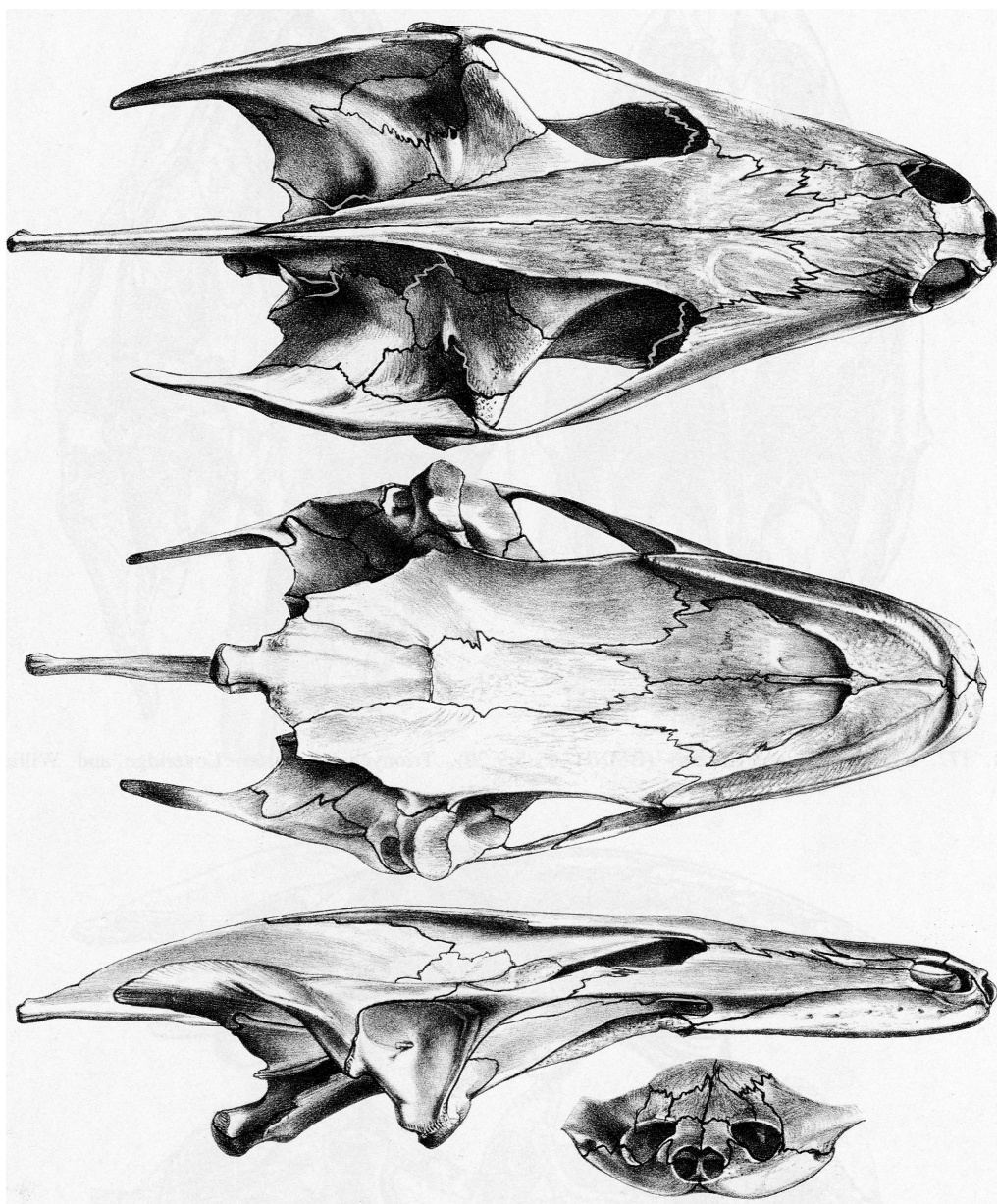


FIG. 176. *Chitra indica* (presumably BMNH specimen, sutures added from MCZ 29487), Trionychidae. From Gray (1855).

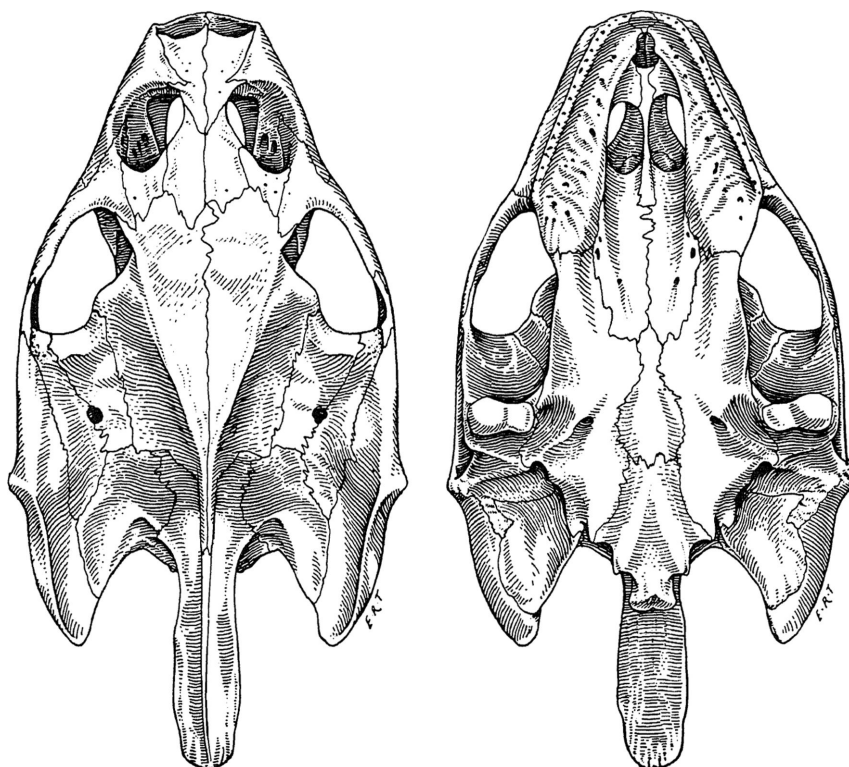


FIG. 177. *Cyclanorbis senegalensis* (BMNH 65.5.9.20), Trionychidae. From Loveridge and Williams (1957).

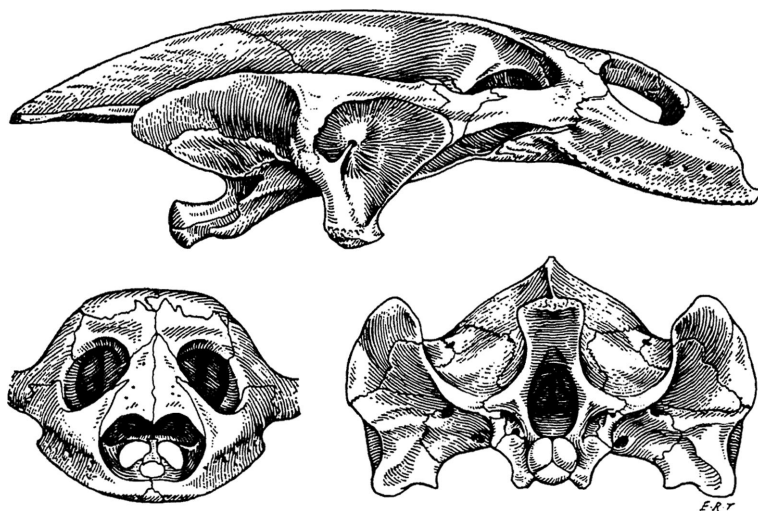


FIG. 178. *Cyclanorbis senegalensis* (BMNH 65.5.9.20), Trionychidae. From Loveridge and Williams (1957).

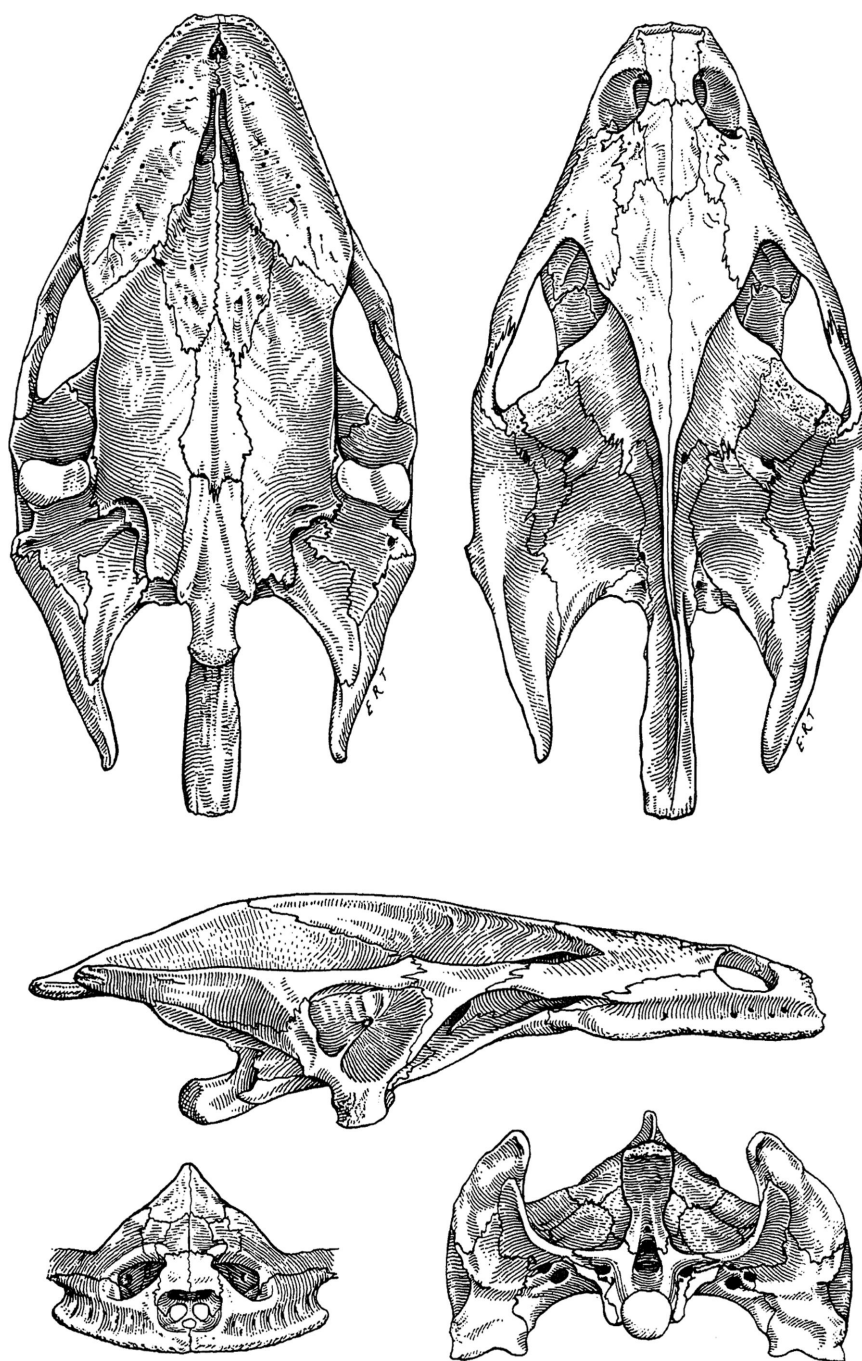


FIG. 179. *Cycloderma frenatum* (BMNH 84.2.4.1; 127 mm.), Trionychidae. From Loveridge and Williams (1957).

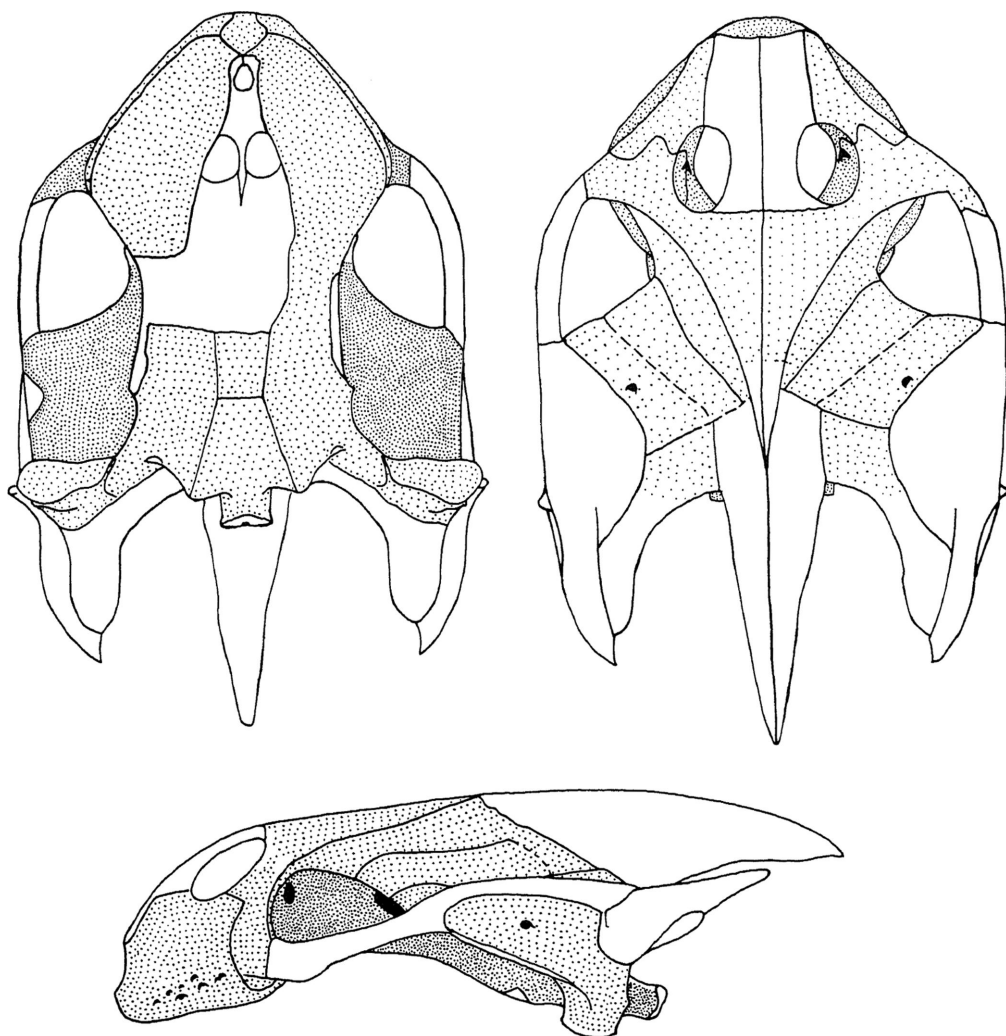


FIG. 180. *Eurycephalochelys fowleri* (BMNH R 8445; 160 mm.), Trionychidae, Bracklesham Beds, lower Eocene, East Wittering, Sussex, England. From Moody and Walker (1970), *q. v.* for other figures and description.

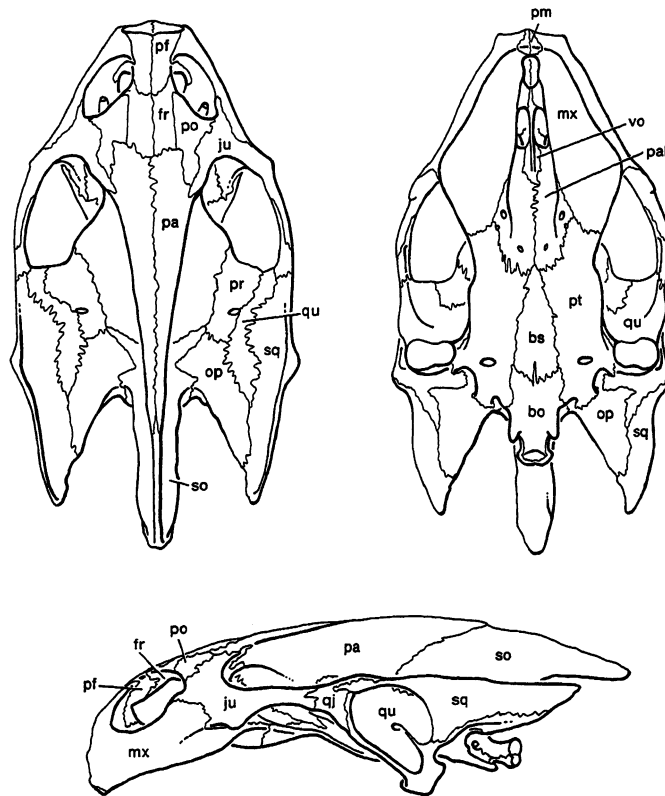


FIG. 181. *Lissemys punctata* (NMNH 61094; 61 mm.), Trionychidae, Madras, India. Basisphenoid and surrounding area restored from MCZ 61093.

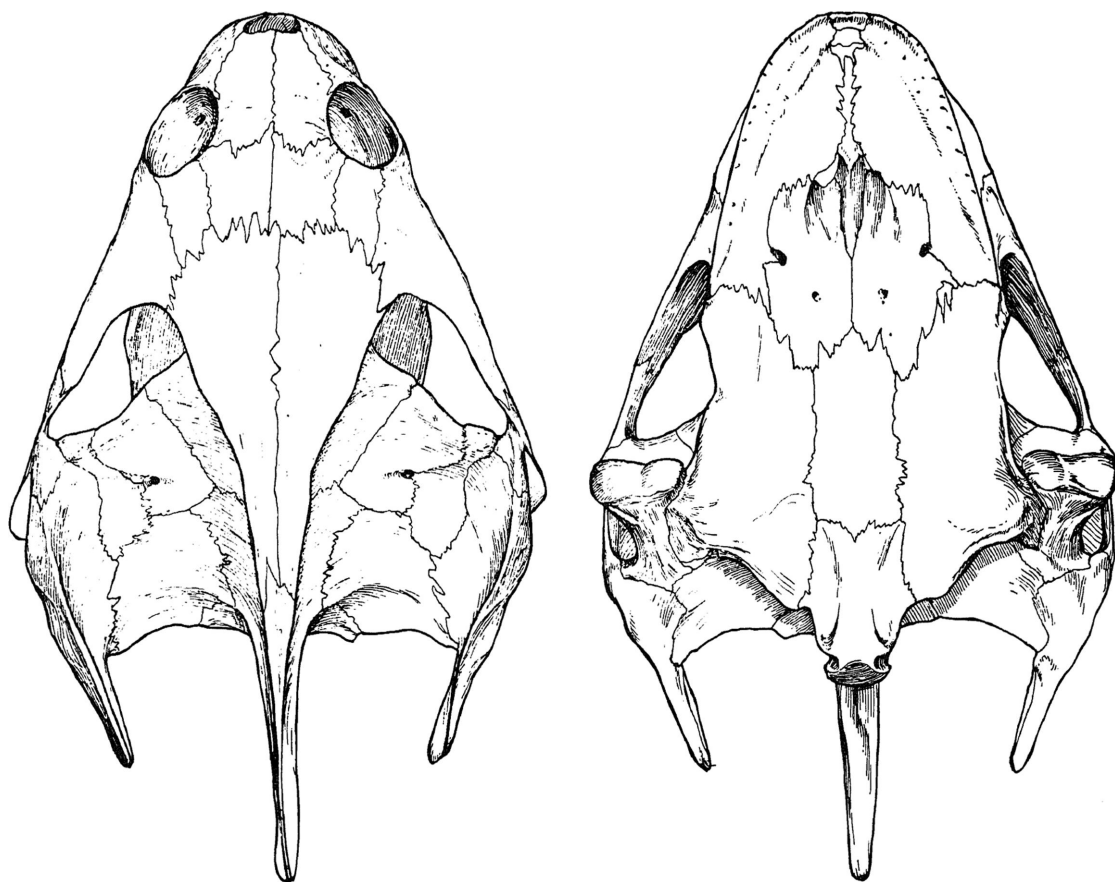


FIG. 182. *Pelochelys bibroni* (AMNH 28342; 88 mm.), Trionychidae, Nodda, Hainan Island, Kwangtung Province, Peoples' Republic of China. From Pope (1935).

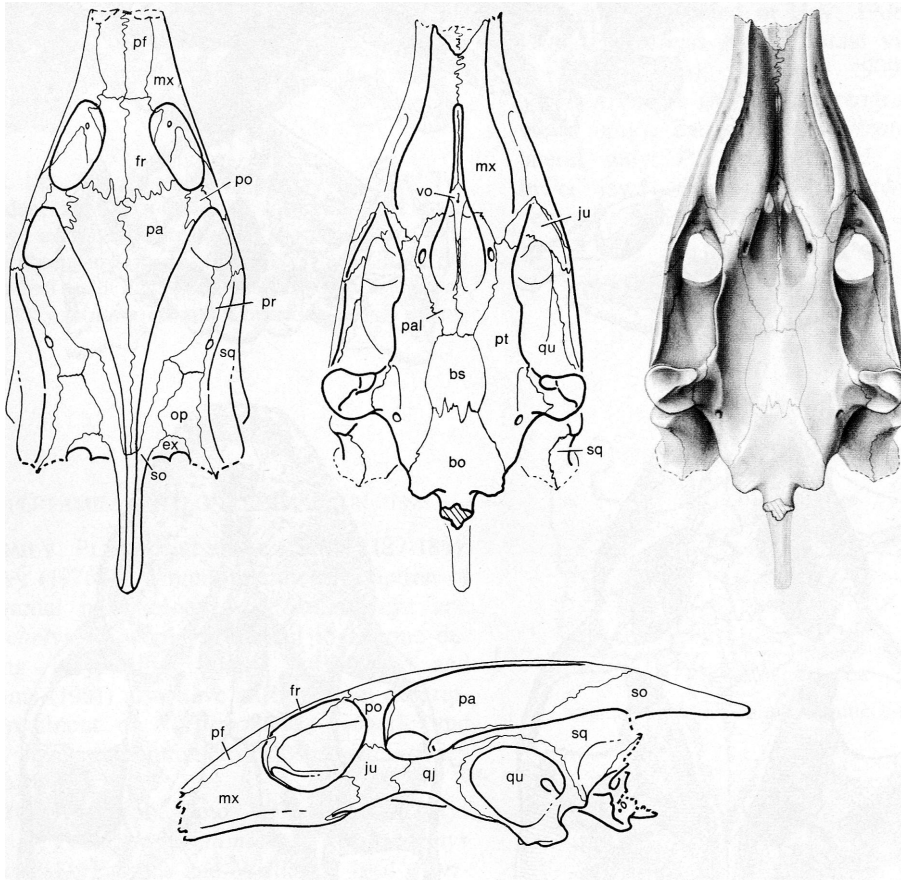


FIG. 183. *Plastomenus thomasi* (AMNH 6015; 47 mm.), Trionychidae, Bridger Formation, Eocene, Grizzly Buttes West, Bridger Basin, Wyoming. Partially restored, see also Hay (1908a, pp. 475-476). Identified by Hay (*ibid.*) on the basis of a hypoplastral fragment associated with this skull.

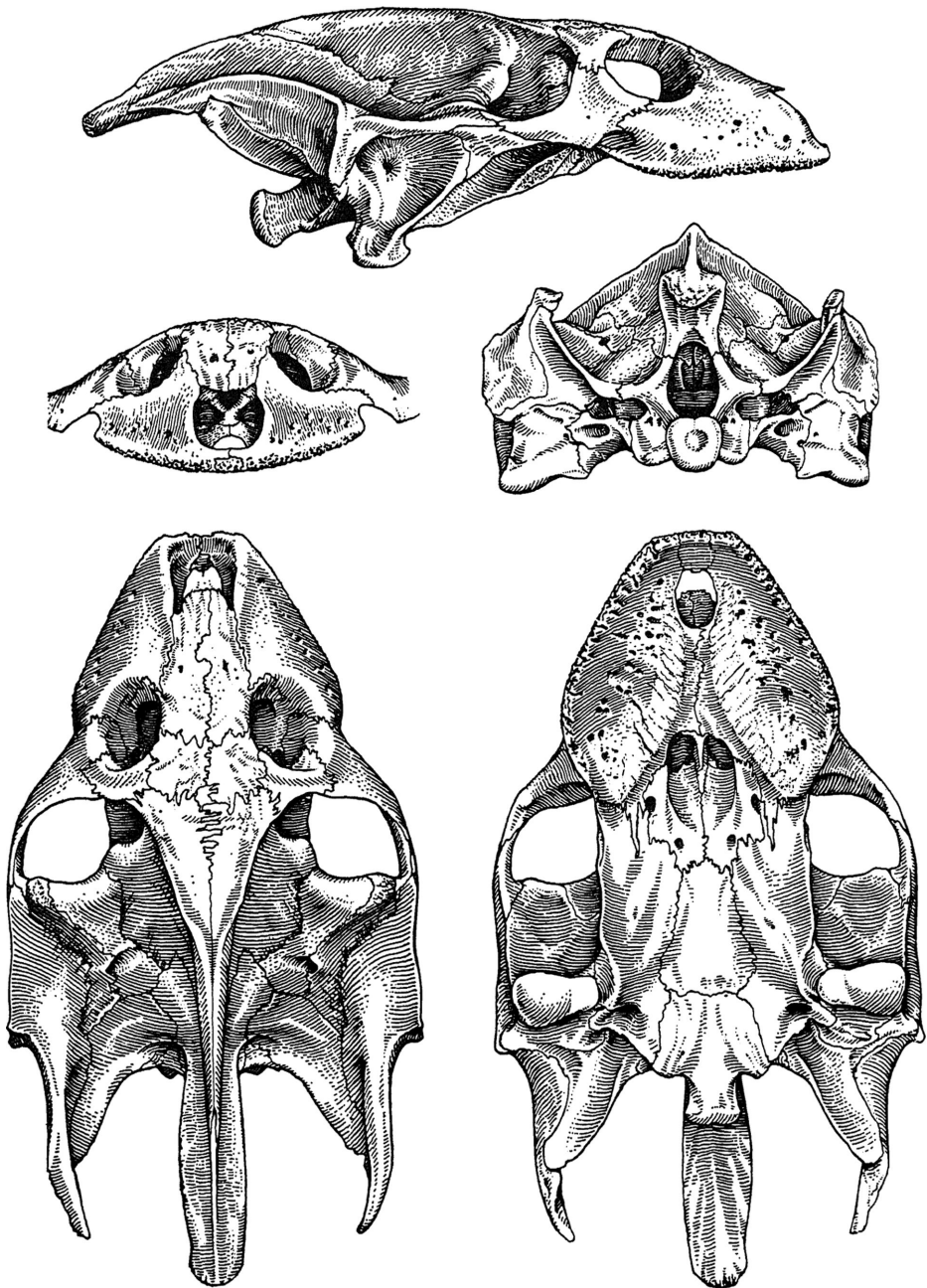


FIG. 184. *Trionyx triunguis* (BMNH 1947.3.6.12; 106 mm.), Trionychidae. Modified from Loveridge and Williams (1957).

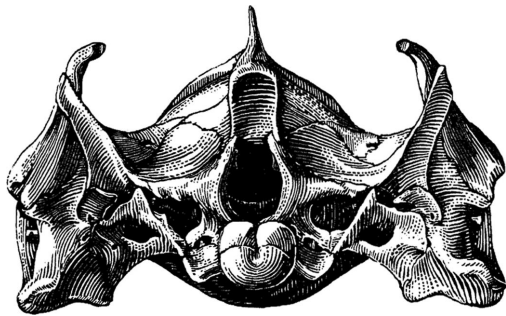


FIG. 185. *Trionyx triunguis* (AMNH 36599), Trionychidae, no data. Occipital view showing rudimentary ascending pterygoid processes that are usually absent in *Trionyx*, *Pelochelys*, and *Chitra* but present and well developed in *Lissemys*, *Cyclanorbis*, and *Cycloderma*. From Loveridge and Williams (1957).

SUPERFAMILY CHELONIOIDEA BAUR, 1893

FAMILY PLESIOCHELYIDAE (FIGS. 187-189): Gaffney (1976) is a monographic description of the cranial morphology of *Portlandemys* and *Plesiochelys*. It would be useful to anyone describing cryptodire skulls. Parsons and Williams (1961) also have an important descriptive treatment of *Portlandemys*. Generic and family level taxonomy is discussed in Gaffney (1975b).

Gaffney, 1975b, and 1976 (*Plesiochelys etalloni**, *Plesiochelys planiceps*, *Portlandemys mcdowellii**); Parsons and Williams, 1961 (*Portlandemys mcdowellii*).

FAMILY PROTOSTEGIDAE (FIGS. 190-193): Zangerl (1953) and Collins (1970) provided the best information on protostegid skulls but Wieland (1900, 1909) should also be consulted. The palate of the protostegines is still inadequately known; although I have used Wieland's (1900) figures they must be considered speculative. I am using Zangerl's (1953) classification of protostegids.

Case, 1896 (*Protostega gigas*, figures of disarticulated braincase elements and lower jaw); Collins, 1970 (*Rhinochelys* sp., braincase; *Rhinochelys pulchriceps*, *R. elegans*, *R. can-*

tabrigensis, photographs and line drawings); Hay, 1908a (*Protostega gigas*, lateral view); Lydekker, 1889 (*Rhinochelys*, dorsal and lateral views); Moret, 1935 (*Rhinochelys amaberti*, dorsal, lateral, and anterior views only); Wieland, 1900 (*Archelon ischyros*, lateral and palatal views*, repeated in Hay, 1908a); Wieland, 1906 (*Protostega gigas*, dorsal view, repeated in Hay, 1908a); Wieland, 1909 (*Protostega copei*, *Archelon ischyros*, photographs of lateral views only); Zangerl, 1953 (*Protostega gigas*, lateral only; *P. dixie*, lateral, dorsal*, and lower jaw*, *Chelosphargis advena*, dorsal*, ventral*, and braincase).

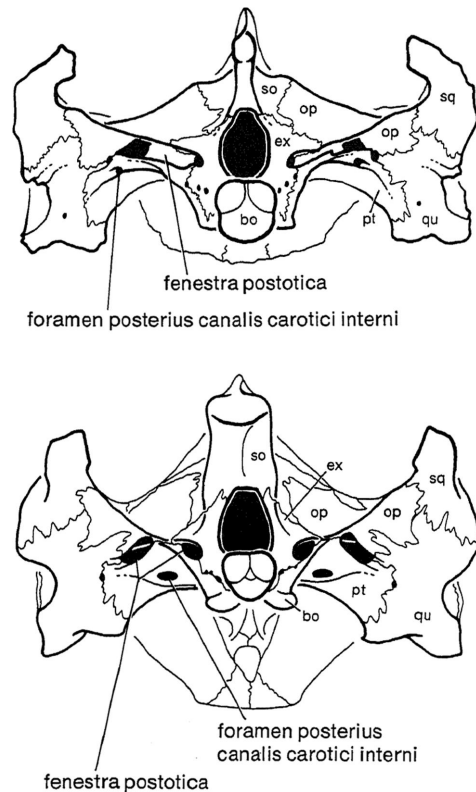


FIG. 186. Occipital views of recent Trionychidae. Upper, *Pelochelys bibroni* (AMNH 23541); lower, *Lissemys punctata* (NMNH 61094).

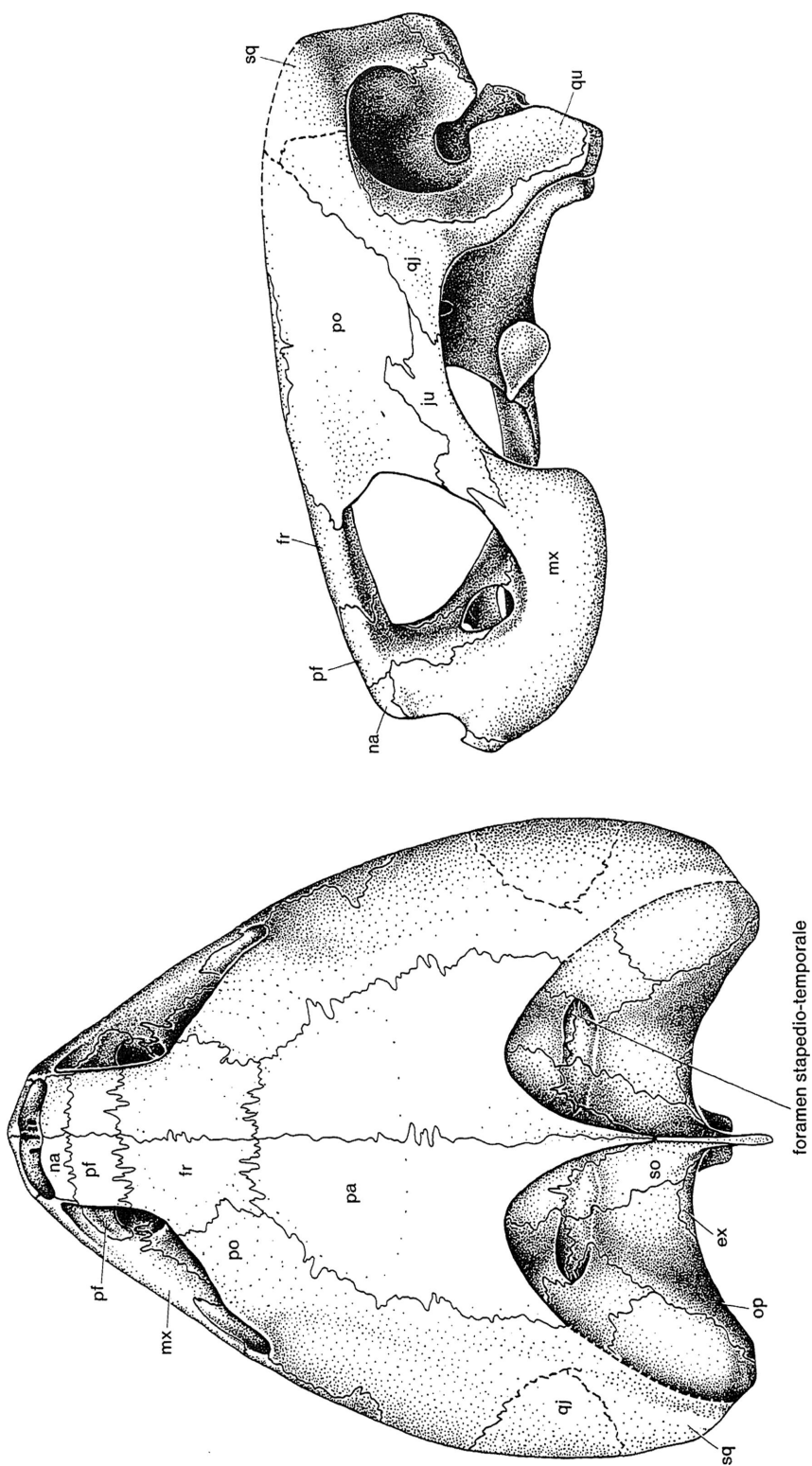


FIG. 187. *Plesiochelys etalloni* (MH 435, near Glovelier; and SM 594, Solothurn; 75 mm. restored), Plesiochelyidae, "Kimmeridge," Late Jurassic, Switzerland. From Gaffney (1975b), *q.v.* for further figures and information.

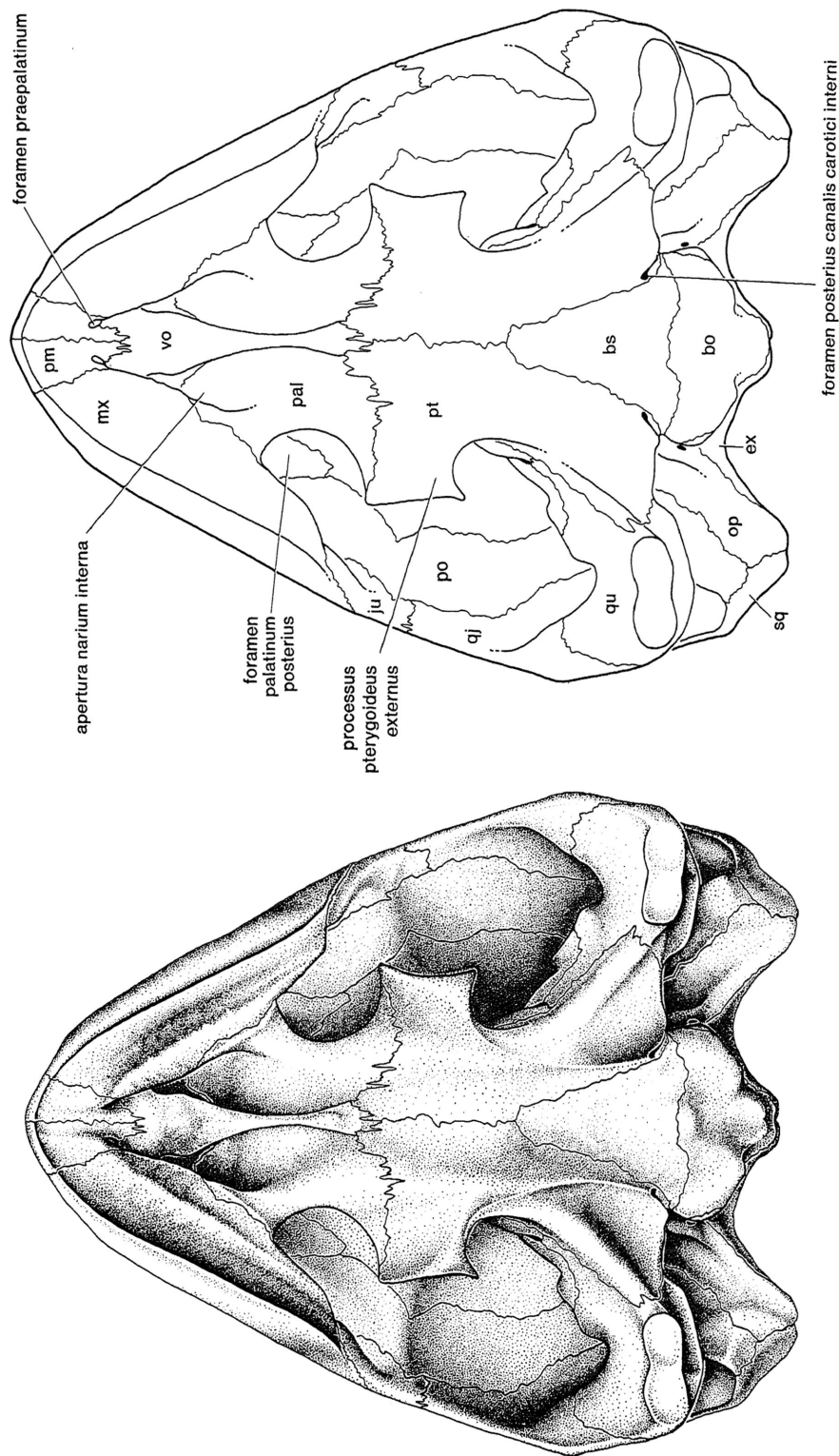


FIG. 188. *Plesiochelys etalloni* (MH 435, near Glovelier; and SM 134, Solothurn; 75 mm. restored), Plesiochelyidae, "Kimmeridge," Late Jurassic, Switzerland. From Gaffney (1975b), q.v. for further figures and information.

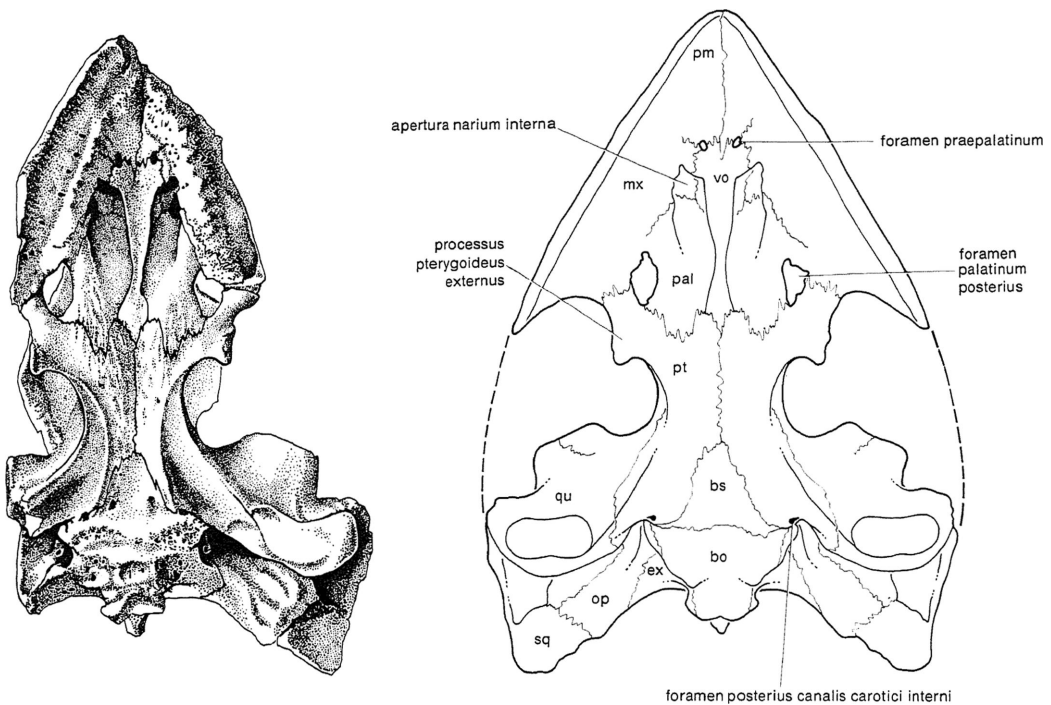


FIG. 189. *Portlandemys mcdowelli* (BMNH R2914), Plesiochelyidae, Portlandian, Late Jurassic, Great Britain. From Gaffney (1975b), *q.v.* for further information.

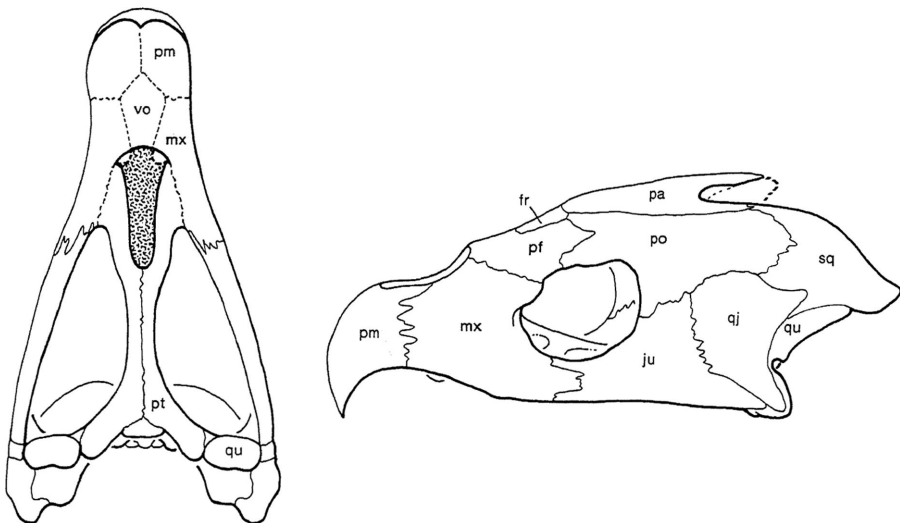


FIG. 190. *Archelon ischyros* (YPM 1783; 720 mm.), Protostegidae, Pierre Formation, Late Cretaceous, near South Fork of Cheyenne River, South Dakota. After Wieland (1900) and specimen. Palatal view is particularly conjectural, lateral crushing has resulted in unknown displacements and sutures are speculative.

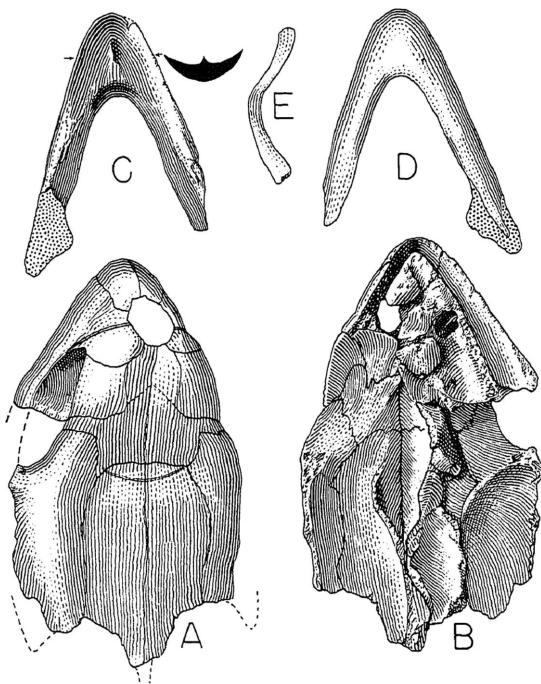


FIG. 191. *Chelosphargis advena* (KU 1219), Protostegidae, exact data lacking but presumably from the Niobrara Formation, late Cretaceous, Kansas. A. Dorsal view of skull. B. Ventral view of skull as preserved. C. Dorsal view of lower jaw with cross section. D. Ventral view of lower jaw. E. Hyoid. From Zangerl (1953).

FAMILY TOXOCHELYIDAE (FIGS. 194-200): Zangerl (1953) has a good description of *Toxochelys* (the reconstruction of *Toxochelys* in this paper is emended from Zangerl's figures), as well as useful figures of the braincase in *Toxochelys* and *Ctenochelys*. I also use his classification of toxochelyids here.

Hay, 1908a (*Toxochelys latiremis*, *Ctenochelys stenopora* [*Toxochelys elkader*], *Ctenochelys* [*Toxochelys*] *procax*, *Porthochelys laticeps*, *Rhetechelys platyops*); Zangerl, 1953 (*Toxochelys latiremis**, *T. moorevillensis*, braincase; *Ctenochelys procax*, palate* and overall photos; *C. tenuitesta*, braincase; *C. stenopora* and *C. acris*, photographs; *Osteopygis emarginatus*, palate*; photographs); Zangerl, 1971 (*Erquelinnesia gosseleti**).

FAMILY DERMOCHELYIDAE (FIGS. 201-205): The unusual nature of *Dermochelys* has made it one of the best known and most widely illustrated species of chelonians. Two monographs are of particular importance: Nick (1912) and Wegner (1959). Nick uses photographs to illustrate the osteology but the colored transverse sections showing soft structures are especially notable. Also in color is a series (*Chelydra*, *Chelonia*, *Dermochelys*) of sagittal sections showing cartilaginous structures. Wegner's work includes a very useful series of plates of disarticulated skulls. Many important structures are unidentified and a few labels are incorrect, however. Schumacher's (1973) study and Nick (1912) are more reliable for soft part identification.

Boulenger, 1889 (*Dermochelys coriacea*, repeated in Smith, 1931, and in Wermuth and Mertens, 1961); Deraniyagala, 1939 (*Dermochelys coriacea*, includes figures of early cranial ossification); Ernst and Barbour, 1972 (*Dermo-*

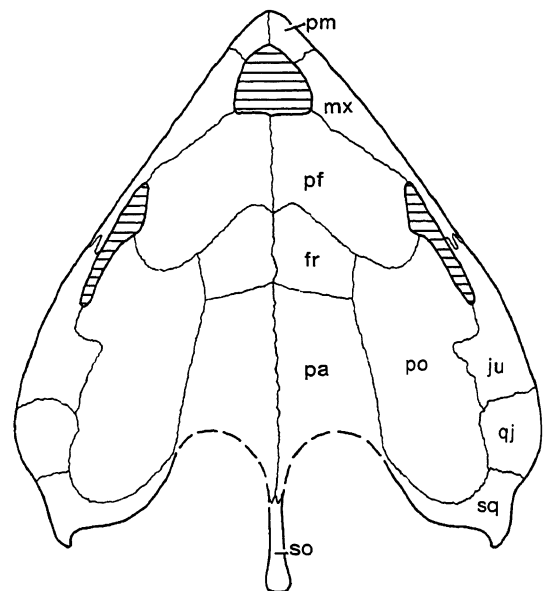


FIG. 192. *Protostega dixie*, Protostegidae, Mooreville Chalk, Selma Formation, Late Cretaceous, Alabama. Reconstruction of skull roof. From Zangerl (1953).

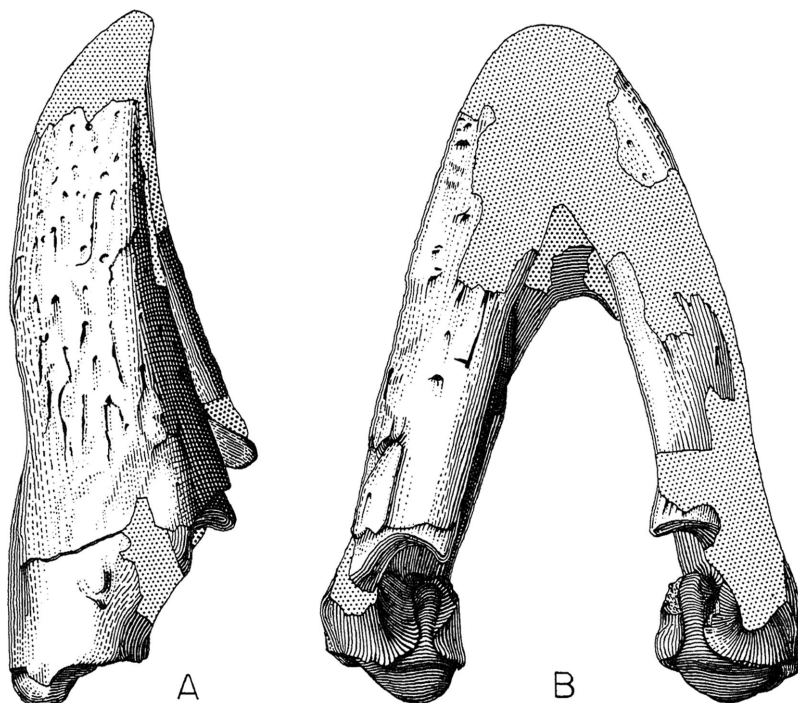


FIG. 193. *Protostega dixie* (FMNH P27385), Protostegidae, Mooreville Chalk, Selma Formation, Late Cretaceous, near Eutaw, Greene County, Alabama. A. Lateral and B. Dorsal views of lower jaw. Total length about 225 mm. From Zangerl (1953).

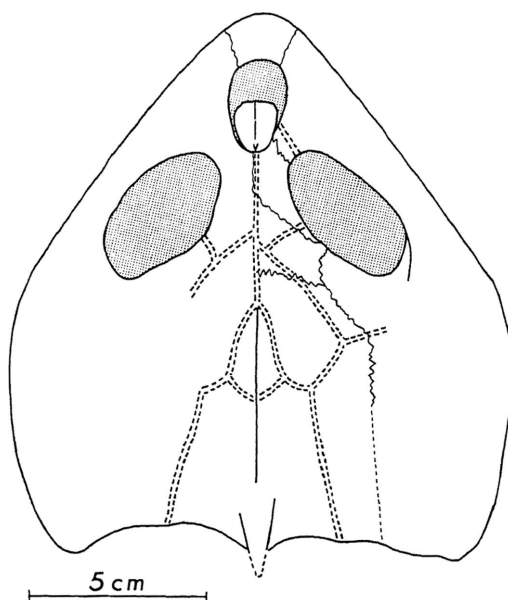


FIG. 194. *Erquelinnesia gosseleti*, Toxochelyidae, Landenian Sands, Eocene, Erquelinnes (Hainaut), Belgium. Dorsal view of skull restored from various specimens. From Zangerl (1971).

chelys coriacea, good quality photographs); Gervais, 1872 (*Dermochelys coriacea** [*Sphargis luth*] also juvenile skull figures); Nick, 1912 (*Dermochelys coriacea*, good quality photographs of intact and partially disarticulated skulls, sagittal section with cartilage*, and a series of transverse sections of head with soft structures labeled); Nielsen, 1959 (*Eosphargis breineri**); Packard, 1940 (*Psephophorus* (?) *oregonensis*); Schumacher, 1973 (*Dermochelys coriacea*, detailed study of soft structures in head, includes arteries and

nerves with aspect of osteology); Wegner, 1959 (*Dermochelys coriacea*, a large monograph with more illustrations than Nick, includes views of disarticulated elements).

FAMILY CHELONIIDAE (FIGS. 206-216): Kesteven (1910) described and figured *Chelonia mydas* in what is probably the most detailed description of a Recent turtle skull in English. Although the figures lack an aesthetic polish they are accurate and very useful; nearly all the bones are disarticulated and individually figured from different views. Nick (1912) discussed

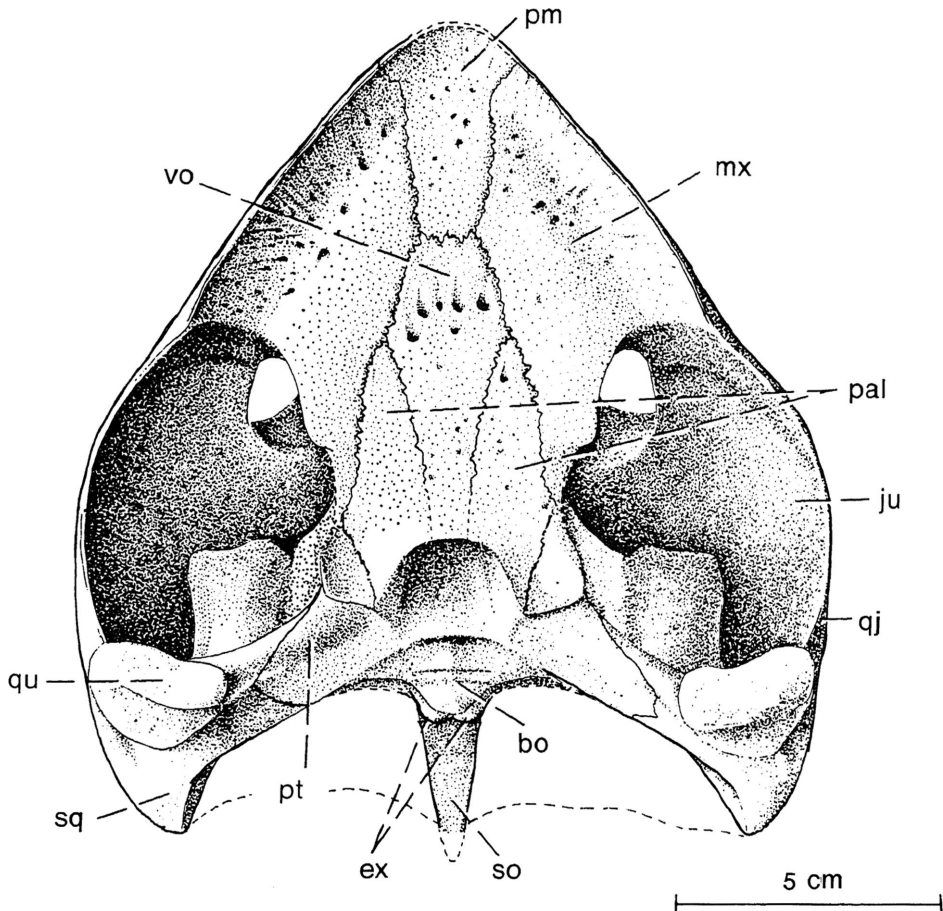


FIG. 195. *Erquelinnesia gosseleti* (IRSNB 1563), Toxochelyidae, Landenian Sands, Eocene, Erquelinnes (Hainaut), Belgium. Partially restored palatal view with some sutures from CM 3426. From Zangerl (1971).

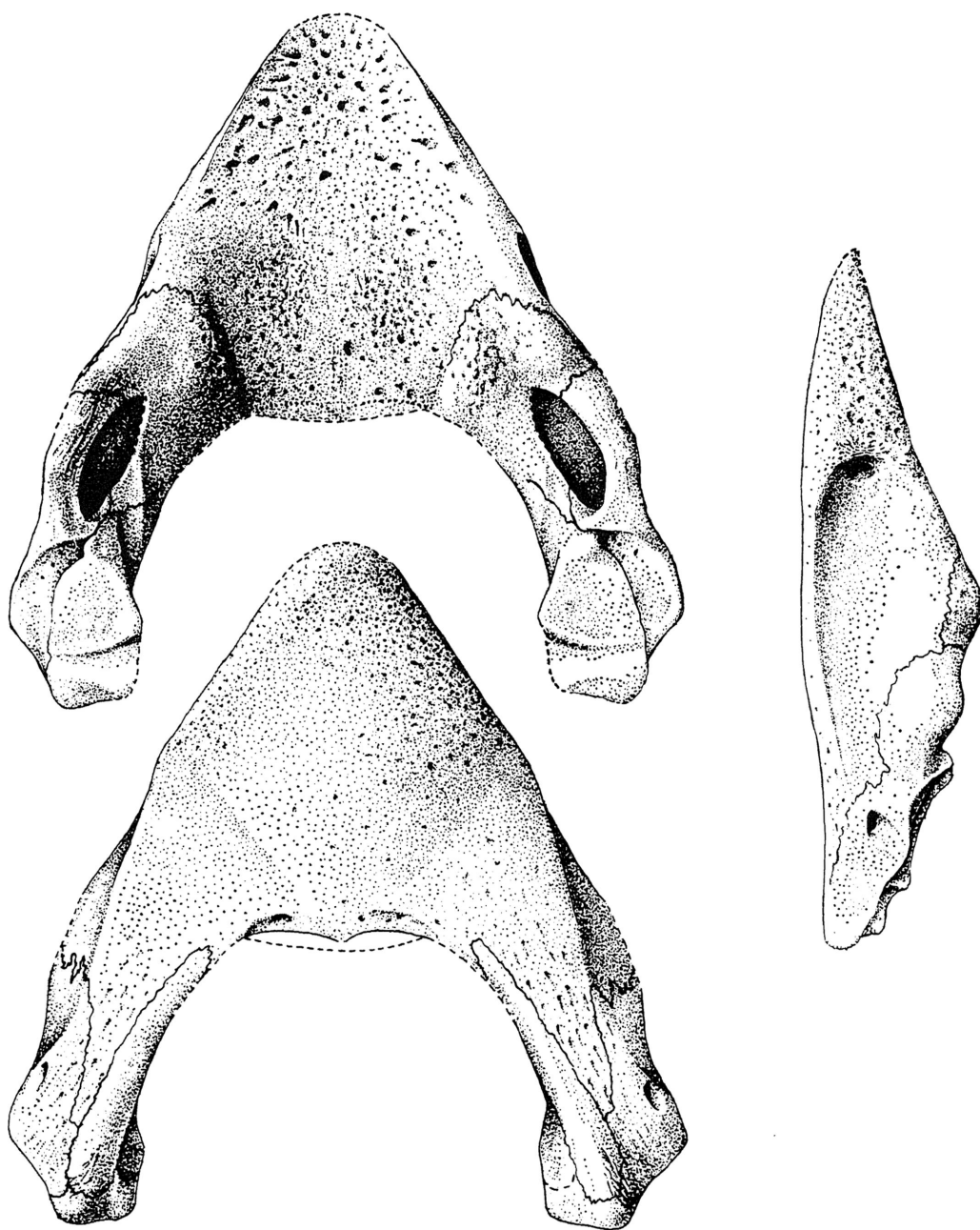


FIG. 196. *Erquelinnesia gosseleti* (IRSNB 1563), Toxochelyidae, Landenian Sands, Eocene, Erquelinnes (Hainaut), Belgium. Lower jaw. From Zangerl (1971).

many aspects of the cheloniid basicranium and has a series of transverse sections (in color) through the head of *Chelonia mydas*. Soliman (1964) has an extensive series of transverse sections and a description and figure (in color) of the cranial nerves in *Eretmochelys imbricata*. Wegner (1959) compared and described some aspects of cheloniid skulls. Albrecht (1976) described cranial arteries and foramina in cheloniids. Somewhat detailed descriptions of fossil cheloniids are available in Zangerl (1960,

basicranium of *Corsochelys*), Casier (1968, also included comparison with *Chelonia mydas*) and, especially Moody (1974).

I have followed Carr (1952) for Recent cheloniid systematics with the addition of *Chelonia depressa* fide Williams, Grandison, and Carr (1967) and Bustard and Limpus (1969). Rebel (1974) has a very useful annotated bibliography; see also Deraniyagala (1939) and Brongersma (1972). For fossil forms see Hay (1908a).

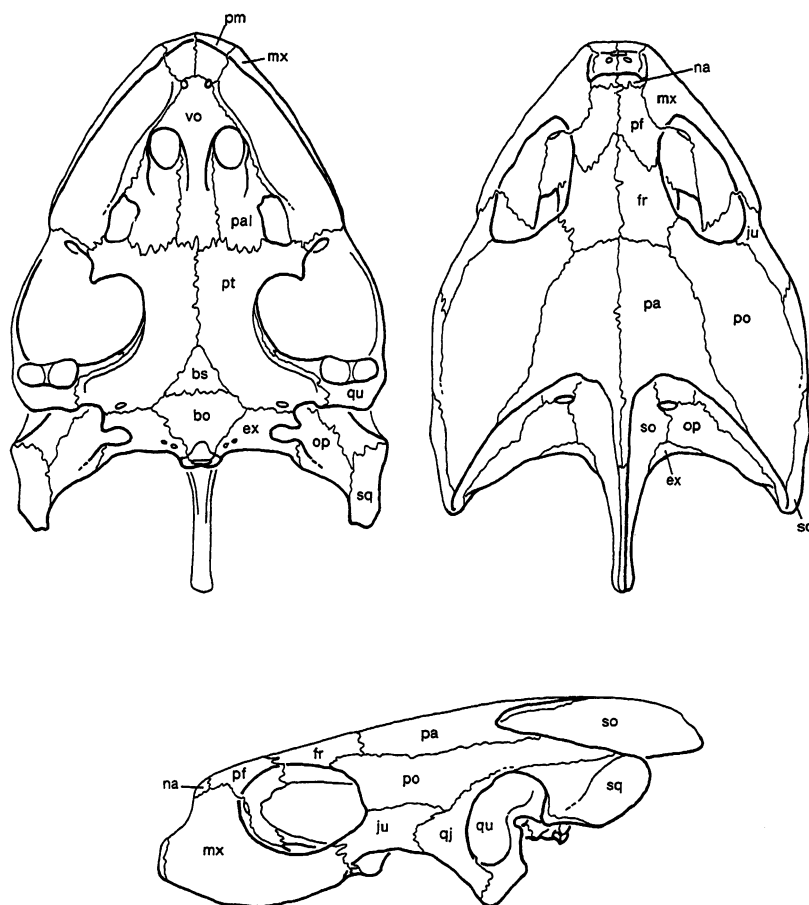


FIG. 197. *Toxochelys latiremis* (based primarily on AMNH 5118; 120 mm.), Toxochelyidae, Niobrara Formation, Late Cretaceous, Butte Creek, Logan County, Kansas. See Zangerl (1953) for other figures and description.

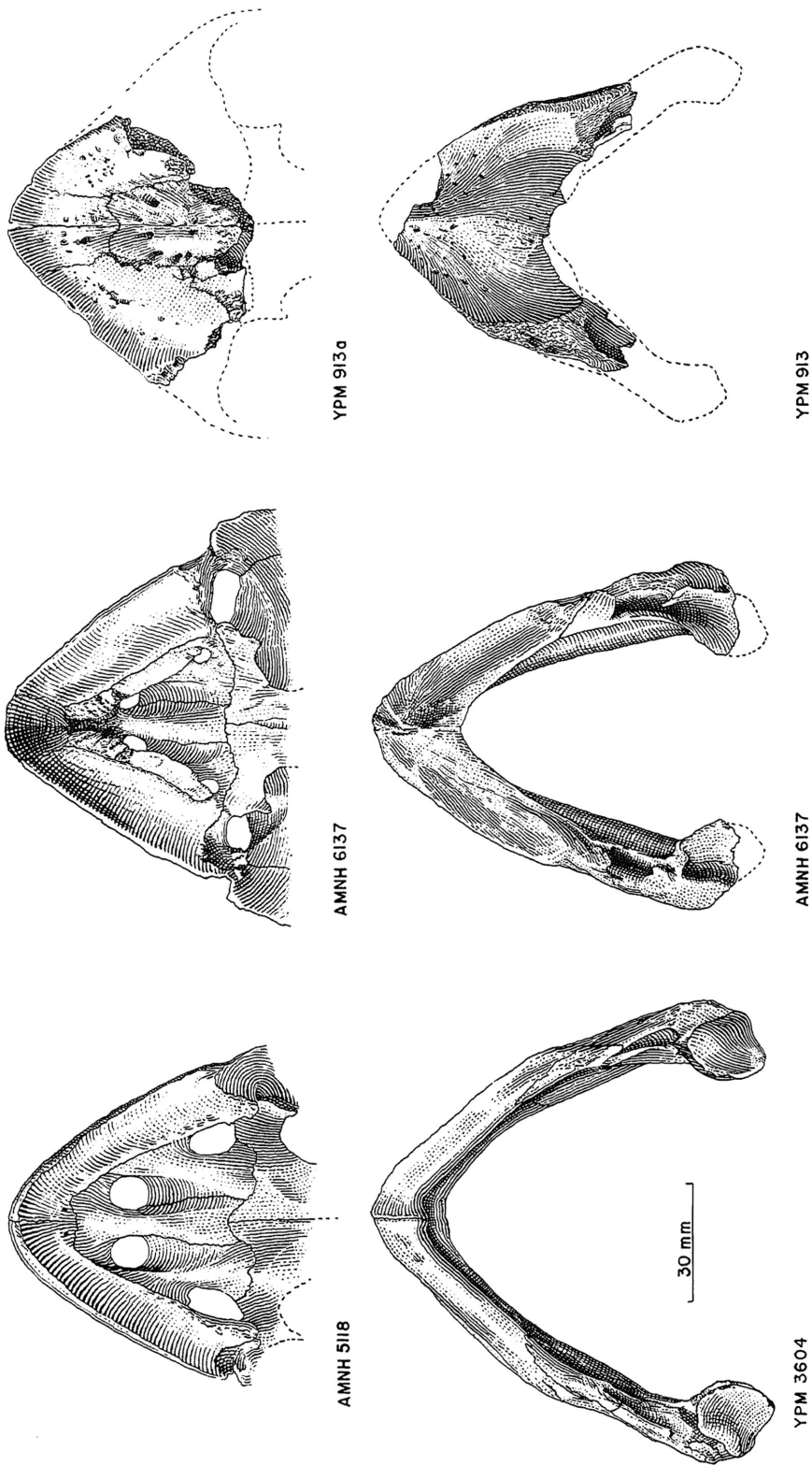


FIG. 198. Comparison of toxochelyid palates (upper row) and lower jaws (lower row). All from the Cretaceous of North America. *Toxochelys* has a primary palate, characteristic of Zangerl's Toxochelyinae; *Ctenochelys* has an incipient secondary palate characteristic of the Ctenochelyinae; and *Osteopygis* has an advanced secondary palate characteristic of the Osteopyginae. From Zangerl (1963).

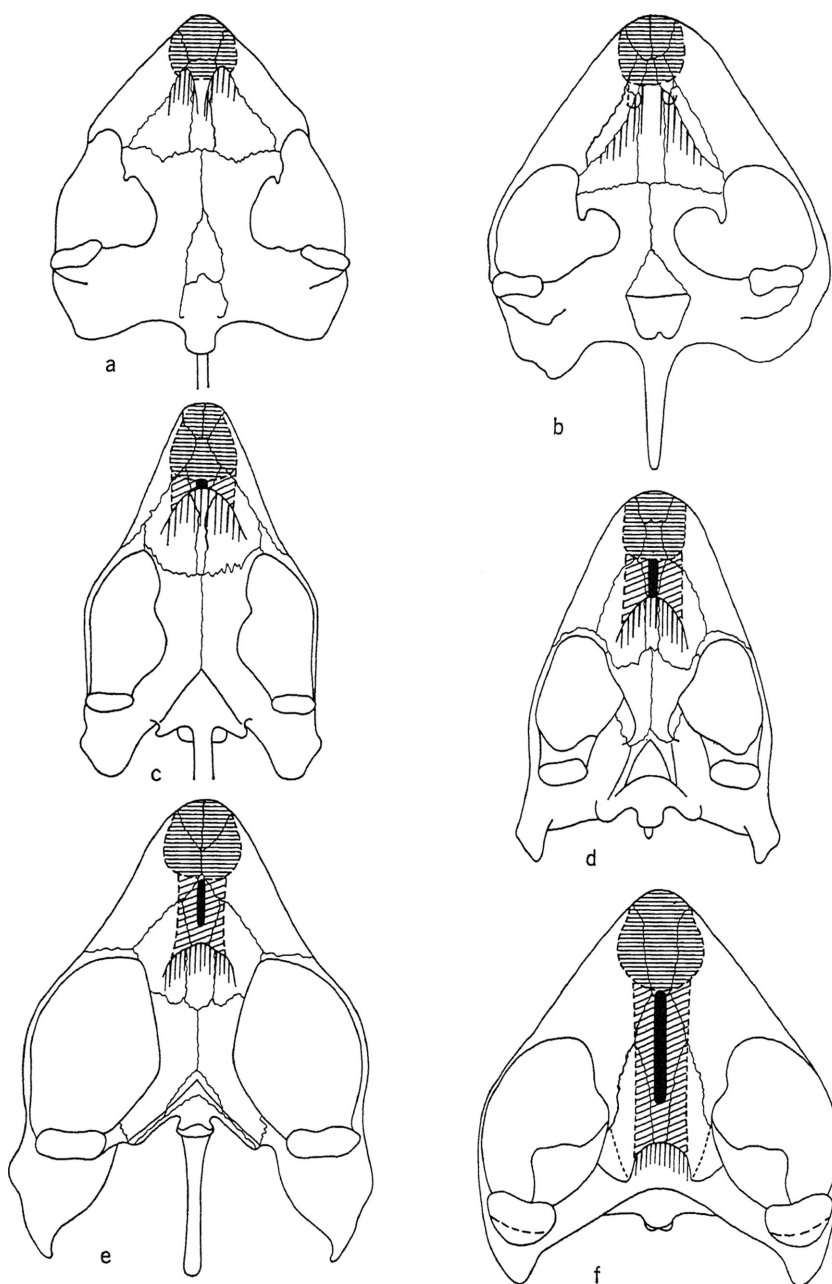


FIG. 199. Comparison of palatal structures in a series of turtles: A. *Chelydra serpentina* (primary palate), Chelydridae, Recent. B. *Ctenochelys procax* (incipient secondary palate), Toxochelyidae, Cretaceous. C. *Eretmochelys imbricata* (secondary palate), Cheloniidae, Recent. D. *Chelonia mydas* (secondary palate), Cheloniidae, Recent. E. *Caretta caretta* (secondary palate), Cheloniidae, Recent. F. *Erquelinnesia gosseleti* (secondary palate), Toxochelyidae, Eocene.

Symbols: horizontal shading, nasal cavity; diagonal shading, nasal passages (meatus choanae), vertical shading, choanal openings (apertura narium interna); black, vomer pillar. From Zangerl (1971); see also Gaffney (1975c) for similar diagram of *Solnhofia*.

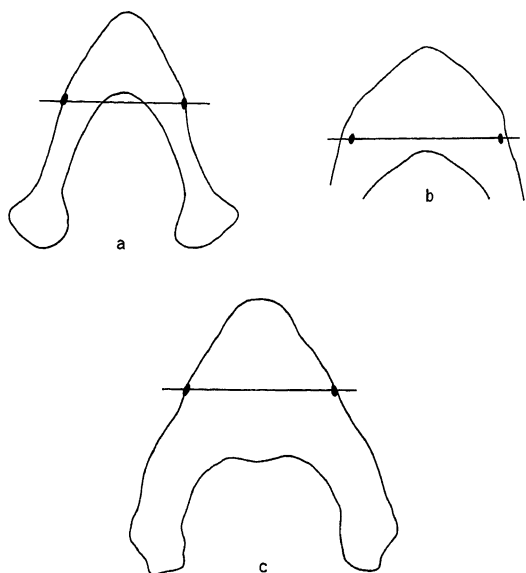


FIG. 200. Comparison of symphysis depths in chelonoids. The lines connect the foramen dentofaciale majus of each ramus. A. *Caretta caretta*, Cheloniidae. B. *Osteopygis emarginatus*, Toxochelyidae. C. *Erquelinnesia gosseleti*, Toxochelyidae. From Zangerl (1971).

Albrecht, 1976 (*Chelonia mydas*); Boulenger, 1889 (*Eretmochelys imbricata*, repeated in Smith, 1931, and Wermuth and Mertens, 1961); Bourret, 1941 (*Eretmochelys imbricata*, *Chelonia mydas*, *Lepidochelys* [*Caretta*] *olivacea*); Carr, 1942 (*Caretta caretta*, *Lepidochelys olivacea*, palates only); Carr, 1952 (*Eretmochelys imbricata*, *Caretta caretta*, *Lepidochelys kempii*, *Chelonia mydas*, palates* and lower jaws; also palate and jaws of *Lepidochelys olivacea*); Casier, 1968 (*Eocheilone brabantica*, line drawings and photographs, including anterior and occipital views, basicranial figure inaccurate; *Chelonia mydas*, anterior and occipital views as well as dorsal, lateral, and palatal); Deraniyagala, 1939 (*Chelonia mydas*, *Eretmochelys imbricata*, the above two are only a dorsolateral oblique view, the following two include a palatal view, *Caretta caretta*, *Lepidochelys olivacea*; some of these are repeated in his other papers); Ernst and Barbour, 1972 (*Chelonia mydas*, *Eret-*

mochelys imbricata, *Caretta caretta*, *Lepidochelys kempii*, *L. olivacea*; photographs of variable quality, sutures usually indistinct); Feuer, 1970 (*Chelonia mydas*, *Eretmochelys imbricata*, palate only of latter; figures crude and inaccurate); Fuchs, 1915 (*Eretmochelys* [*Chelone*] *imbricata*, monographic study of chondrocranium with high quality figures of chondrocranium and ossifications); Fuchs, 1931 (*Chelonia mydas*, lower jaw); Fuchs, 1932 (*Eretmochelys* [*Chelone*] *imbricata*, figures of embryo sectioned through processus pterygoideus externus); Gray, 1873d (*Eretmochelys imbricata* [*Onychochelys kraussi*]); Hay, 1908b (*Caretta caretta*, *Lepidochelys* [*Colpochelys*] *kempii*, "*Caretta remivaga*," photographs usually with sutures); Hoffmann, 1890 (*Chelonia mydas*); Kesteven, 1910 (*Chelonia mydas*, many figures of disarticulated and partially articulated elements); Moody, 1974 (*Puppigerus camperi*, includes sagittal section, endocast, and lower jaws); Nick, 1912 (*Chelonia mydas*, a useful colored series of transverse sections, sagittal section showing cartilage structures); Owen and Bell, 1849 (*Puppigerus camperi* [*Chelone longiceps*]*, *Argillochelys* [*Chelone*] *cuneiceps*); Rüschkamp, 1925 (*Allopleuron hoffmanni*, photos of skull but sutures ambiguous); Shindo, 1914 (*Chelonia mydas* [*viridis*], schematic figure of arteries); Siebenrock, 1897 (*Chelonia mydas*, dorsal views of basisphenoid* and pterygoid); Soliman, 1964 (*Eretmochelys imbricata*, transverse sections of the head, more numerous and more detailed than Nick, 1912; also a color figure of the cranial nerves, and a palatal view); Ubaghs, 1883 (*Allopleuron* [*Chelone*] *hoffmanni*, lower jaw photographs); Ubaghs, 1888 (*Allopleuron* [*Chelone*] *hoffmanni*, skull photographs); Wegner, 1959 (*Chelonia mydas*, *Caretta caretta*, occipital and sagittal views, various figures of ethmoid and basicranial areas); Williston, 1894; (*Desmatochelys lowii*, dorsal and palatal* views, repeated in Williston, 1898); Zangerl, 1953 (*Chelonia mydas*, dorsal view of braincase with skull roof removed); Zangerl, 1958 (*Glarichelys knorri*, side and dorsal views only; dorsal views* of the four living genera); Zangerl, 1960 (*Corsochelys hali-*

niches, good figures of basicranium, skull roof*, endocast*); Zangerl and Sloan, 1960 (*Desmatochelys lowii*, dorsal* and lateral).

SUPERFAMILY TESTUDINOIDEA FITZINGER, 1826

FAMILY CHELYDRIDAE (INCLUDING PLATYSTERNIDAE) (FIGS. 216-224): Although chelydrids have not been described in detail,

Nick (1912) provided an important comparison of the basicranium among *Chelydra*, cheloniids, and *Dermochelys*. The transverse sections of *Chelydra* in this paper are also very useful. Soliman (1964) has a more extensive series of sections, with soft structures labeled in more detail, and he figures and describes the cranial nerves. Gaffney (1972b) provided the most detailed series of figures including bas-

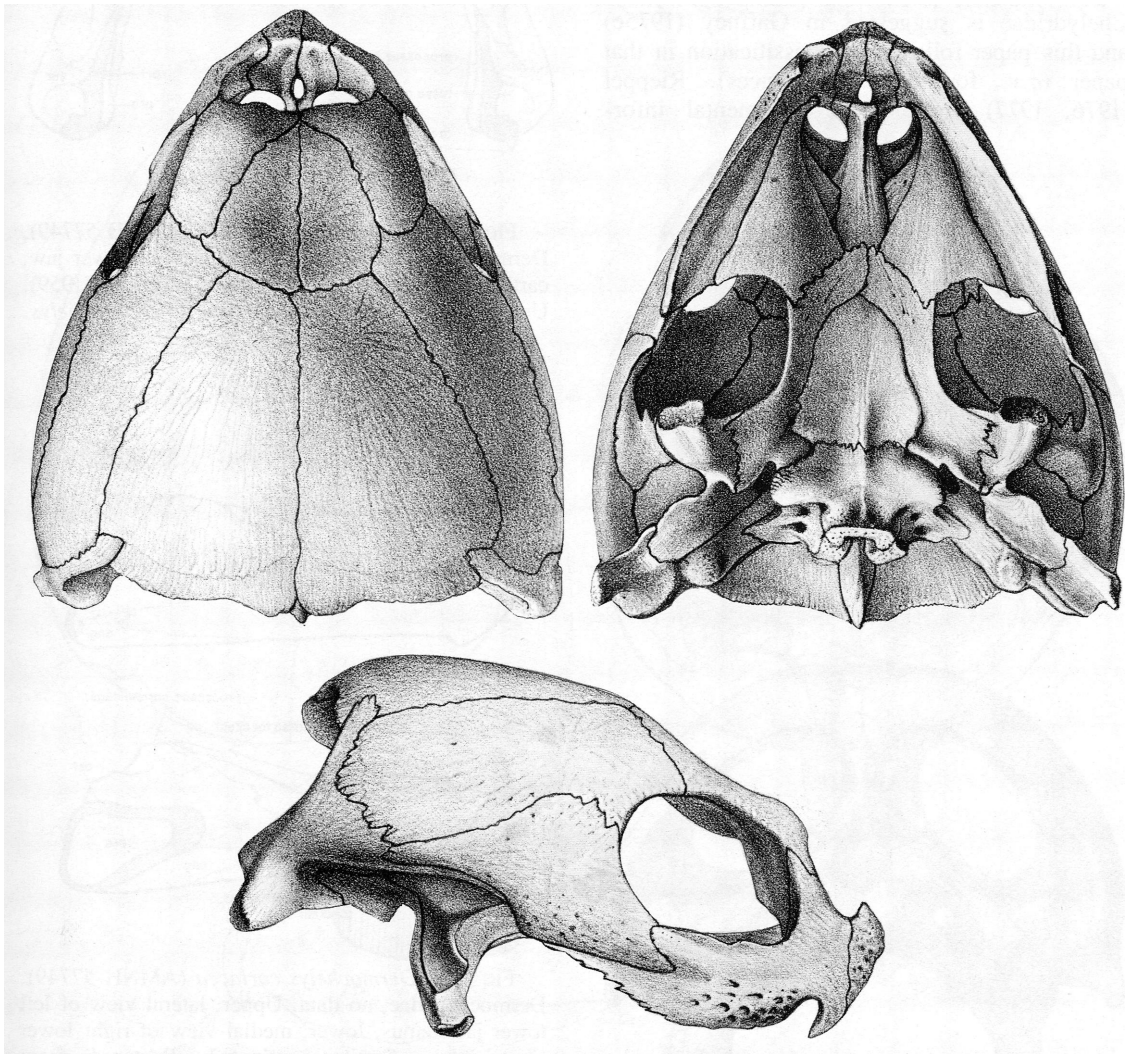


FIG. 201. *Dermochelys coriacea*, Dermochelyidae. Modified from Gervais (1872). For further figures and description see Nick (1912) and Wegner (1959).

icranial foramina, ear structures, and lower jaw (nearly all are repeated in this paper). Albrecht (1976) described the cranial arteries and foramina in *Chelydra*. Gaffney (1975d) also has a series of sections (for comparison with a similar series of sections in a pleurodire, neither series is reproduced here) and good halftones of the neurocranial ossifications in *Chelydra*. Overall skull views are available in Gray (1855), Boulenger (1889), and Gaffney (1975e). My inclusion of *Platysternon* in the Chelydridae is suggested in Gaffney (1975e) and this paper follows the classification in that paper (*q.v.* for earlier references). Rieppel (1976, 1977) presented developmental infor-

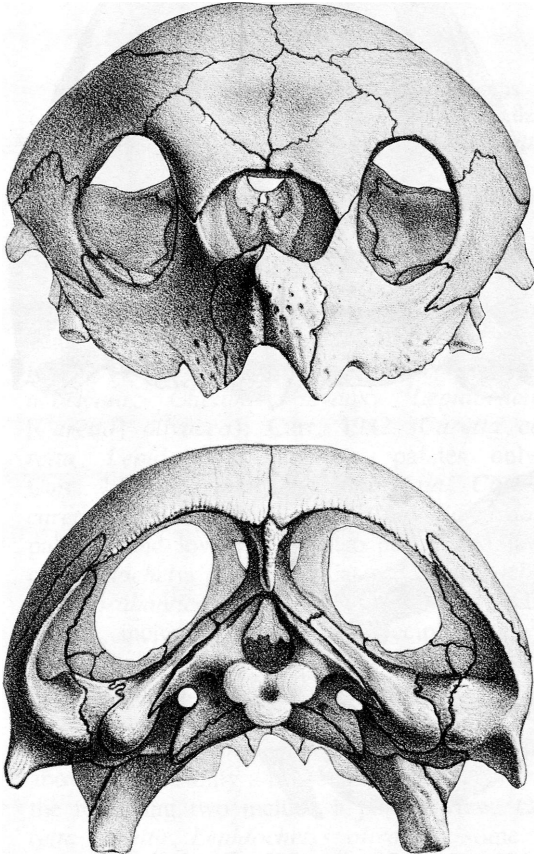


FIG. 202. *Dermochelys coriacea*, Dermochelyidae. Modified from Gervais (1872).

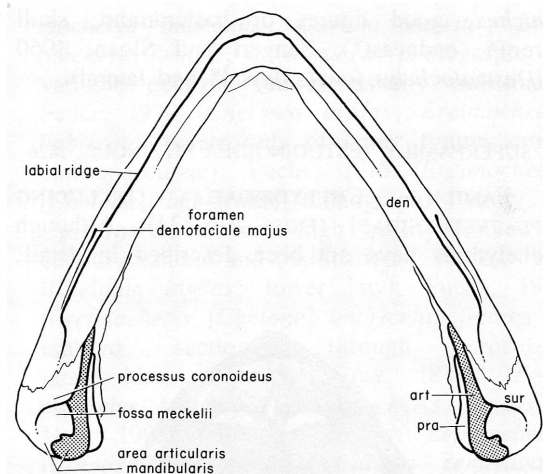


FIG. 203. *Dermochelys coriacea* (AMNH 57749), Dermochelyidae, no data. Dorsal view of lower jaw, cartilage stippled. Restored from Wegner (11959). Unossified articular is characteristic of *Dermochelys*.

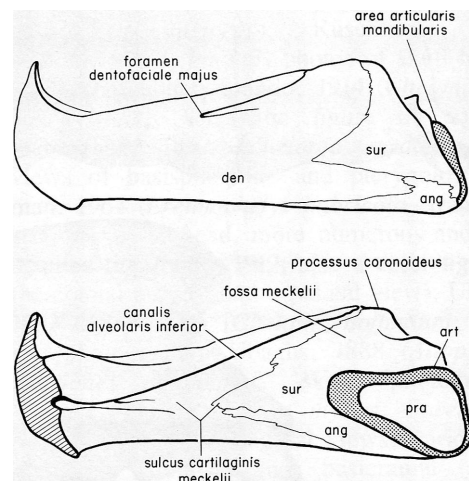


FIG. 204. *Dermochelys coriacea* (AMNH 57749), Dermochelyidae, no data. Upper, lateral view of left lower jaw ramus; lower, medial view of right lower jaw ramus. Cartilage stippled. Restored from Wegner (1959). See also Poglayen-Neuwall (1953) for medial view of jaw with cartilage and nerves indicated.

mation on the chondrocranium in *Chelydra*.

Albrecht, 1976 (*Chelydra serpentina*, arteries and canals); Ashley, 1955 (*Chelydra serpentina*); deBeer, 1926 (*Chelydra serpentina*, embryo chondrocranium with nerves and vessels); Boulenger, 1889 (*Platysternon megacephalum*, *Chelydra serpentina*, *Macrolemys temminckii*, repeated in Wermuth and Mertens, 1961); Bourret, 1941 (*Platysternon megacephalum*); Erickson, 1973 (*Protochelydra zangerli**); Ernst and Barbour, 1972 (*Chelydra*

serpentina, *C. osceola*, *Macrolemys temminckii*; photographs of variable quality, sutures usually indistinct); Feuer, 1970 (*Macrolemys temminckii*, figures crude and inaccurate); Gaffney, 1975d (*Chelydra serpentina*, neurocranial and braincase figures* and a series of transverse sections); Gaffney, 1975e (*Chelydra serpentina**, *Macrolemys temminckii**, *Platysternon megacephalum**); Gray, 1855 (*Chelydra serpentina*, *Macrolemys temminckii*; high quality halftones); Hanson, 1919

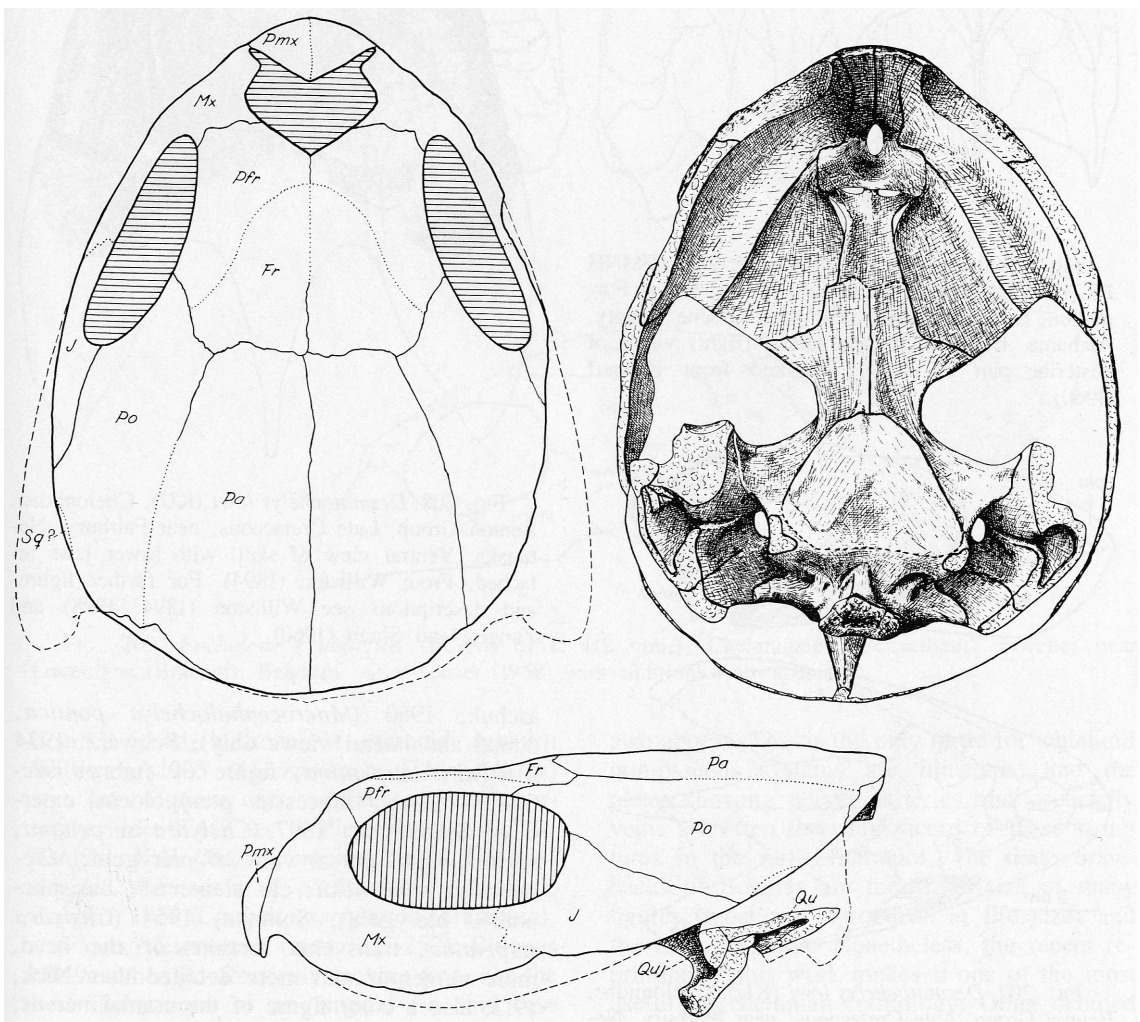


FIG. 205. *Eosphargis breineri* (Fur Museum, Nederby, Denmark) Dermochelyidae, Mo Clay Formation, early Eocene, near Limfjord, Denmark. Modified from Nielsen (1959), *q.v.* for description and other figures.

(*Chelydra serpentina*, cranial nerves); Nick, 1912 (*Chelydra serpentina*, a series of transverse sections in color and a sagittal section showing cartilage*); Pidoplichko and Tar-

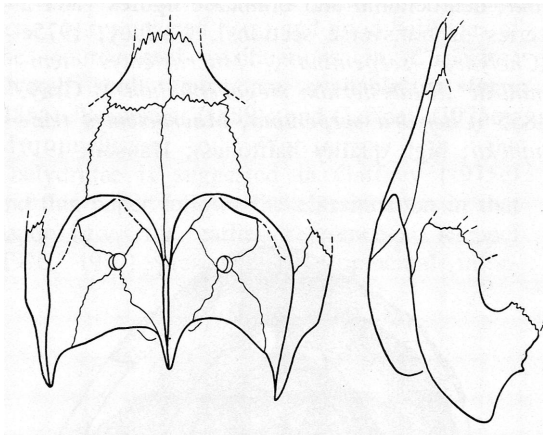


FIG. 206. *Corsochelys haliniches* (FMNH PR249), Cheloniidae, Mooreville Chalk, Selma Formation, Late Cretaceous, near West Greene County, Alabama. Dorsal (left) and lateral (right) views of posterior part of skull. Modified from Zangerl (1960).

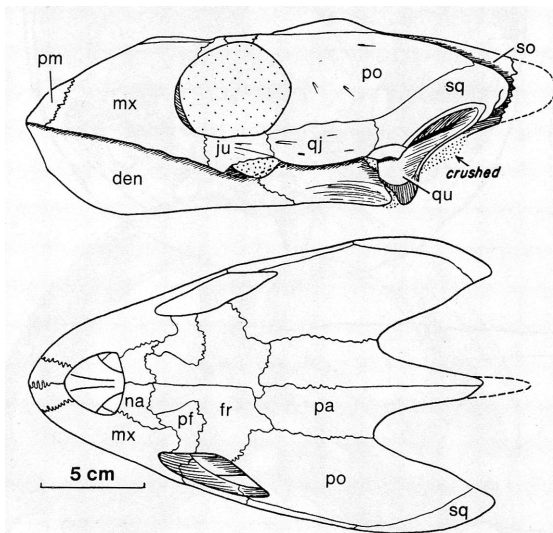


FIG. 207. *Desmatochelys lowi* (KU), Cheloniidae, Benton Group, Late Cretaceous, near Fairbury, Nebraska. Reinterpretation by Eaton in Zangerl and Sloan (1960) of specimen described in Williston (1894). From Zangerl and Sloan (1960).

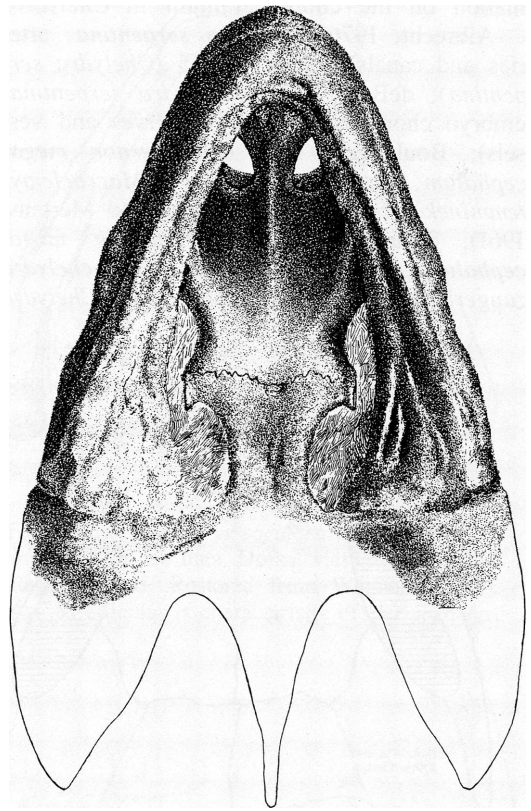


FIG. 208. *Desmatochelys lowi* (KU), Cheloniidae, Benton Group, Late Cretaceous, near Fairbury, Nebraska. Ventral view of skull with lower jaws attached. From Williston (1894). For further figures and descriptions see Williston (1894, 1898) and Zangerl and Sloan (1960).

aschuk, 1960 (*Macrocephalochelys pontica*, dorsal and lateral views only); Schwarz, 1934 (*Chelydra serpentina*, figure of embryo sectioned through processus pterygoideus externus); Siebenrock, 1897 (*Chelydra serpentina*, sagittal view, dorsal view of pterygoid, *Macrolemys temminckii*, ear elements*, basisphenoid*, pterygoid); Soliman, 1964 (*Chelydra serpentina*, transverse sections of the head, more numerous and more detailed than Nick, 1912; also a color figure of the cranial nerves, and a palatal view); Wegner, 1959 (*Macrolemys temminckii*, orbital floor with foramen palatinum posterius mislabeled as "foramen op-

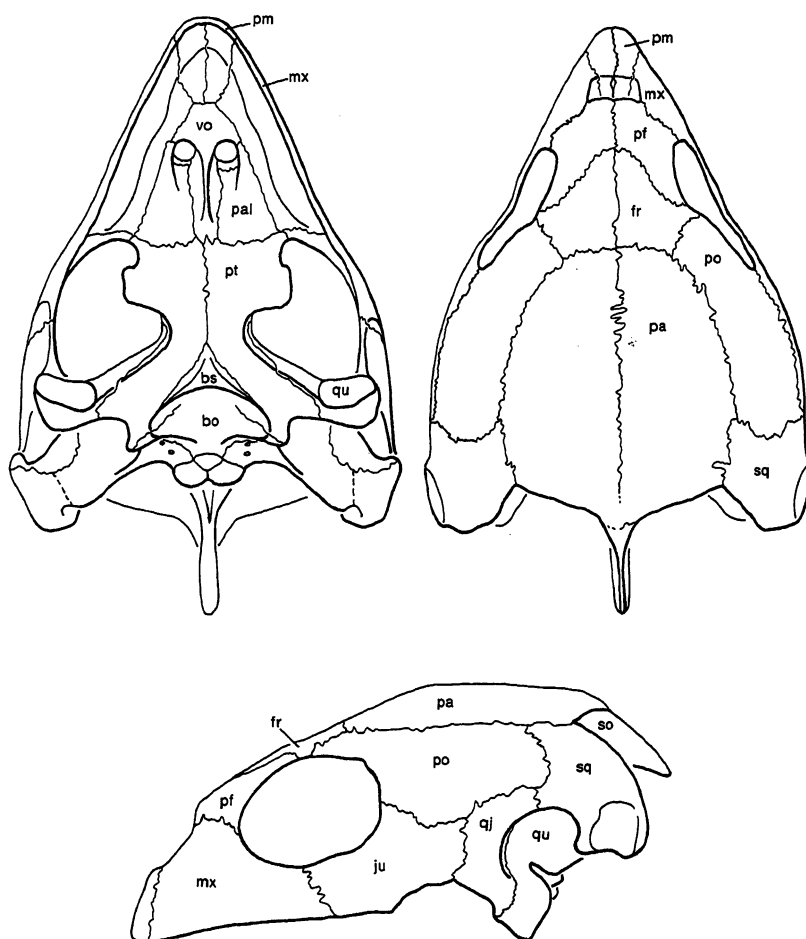


FIG. 209. *Eochelone brabantica* (IRSNB 6152; 112 mm.), Cheloniidae, "Bruxellien," Eocene, near Loupoigne (Brabant), Belgium. After Casier (1968) with additions from specimen.

ticum," good halftone of ethmoid region); Williston, 1925 (*Macrolemys* [*Macrochelys*] sp., lateral view and sagittal section, incorrectly identified as "Pleurodiran skull"); Zangerl, 1945 (*Macrolemys schmidtii*, *M. temminckii*, side view of partial skull of latter); Zangerl, 1953 (*Chelydra serpentina*, braincase).

FAMILY EMYDIDAE (FIGS. 225-257): Bojanus (1819) although effectively lacking text, has the best illustrations of an emydid (in this case *Emys orbicularis*). Nearly all the bones are figured disarticulated as well as partially articulated, and a number of sectioned specimens

also appear. This is the only turtle for which all non-osseous systems are illustrated and the plates showing nerves, arteries and especially veins are often the only record of these structures in the turtle literature. The main drawbacks of Bojanus are the small size of many figures (most are reproduced at life size) and the Latin captions. Nonetheless, the recent reprinting of this work makes it one of the most useful for chelonian craniology. Other detailed morphologic treatments of emydids are much narrower in scope. McDowell (1961) and Albrecht (1967) described cranial arteries and fo-

ramina, Shiino (1913) dealt with cranial nerves, and Siebenrock (1897) came through with a good set of representative ear, pterygoid, and sagittal views. Complete skulls of emydids are illustrated by Gray (1869, repeated in Boulenger, 1889, and Wermuth and Mertens, 1961), Bourret (1941, some of these are the

only available figures of Asian species, others redrawn from Gray but without citations), McDowell (1964), and Ernst and Barbour (1972).

The recognized genera of emydids vary more from author to author than the genera of other recent turtle families. I am using here a

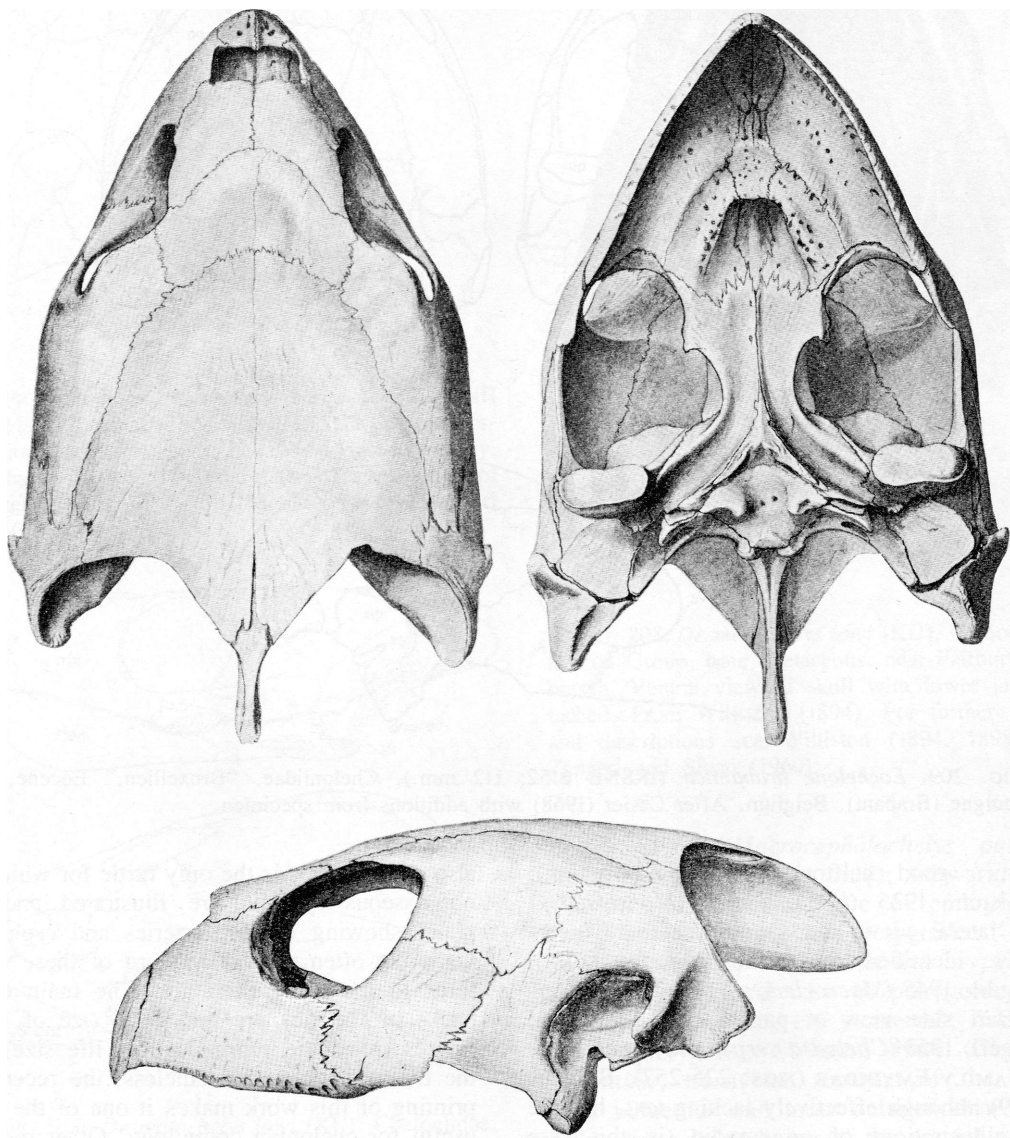


FIG. 210. *Lepidochelys kempi*, Cheloniidae, no data. Modified from Hay (1908a).

combination of Wermuth and Mertens (1961) and McDowell (1964). It seems to me that in cases of doubt an overly "split" classification will more readily allow the development of phylogenetic hypotheses than a "lumped" one. To that end I am using McDowell's (1964) genera except that I am retaining *Malaclemys* distinct from *Graptemys*. His merging of *Pseudemys* and *Chrysemys* has been followed by other workers on this group (Weaver and Rose, 1967; Ernst and Barbour, 1972), and I also follow it. Other aspects of McDowell's classification are discussed in Weaver and Rose (1967), Weaver and Robertson (1967), Milstead (1969), and Bramble (1974). See table 1 for a comparison of the species distribution between McDowell and Wermuth and Mertens. Love-ridge and Williams (1957) contains an impor-

tant and influential phylogeny of emydids but as they deal specifically only with the sparse African emydid fauna their work can not be used as a general reference for synonymies and literature. Other important systematic treatments are Boulenger (1889), Smith (1931), Bourret (1941), and Carr (1952).

Albrecht, 1967 (*Chrysemys scripta*, basicranial arteries and foramina*); Baur, 1896 (*Orlitia borneensis** [*Adelochelys crassa*]); Bogert and Oliver, 1945 (*Terrapene klauberi*, side view only); Bojanus, 1819 (*Emys orbicularis*, figures of disarticulated and partially articulated elements as well as sectioned skull and soft parts, some figures redrawn in Romer, 1956); Boulenger, 1889 (*Heosemys* [*Geoemyda*] *grandis*, repeated in Wermuth and Mertens, 1961); Bourret, 1941 (*Geoemyda* [*Cyclemys*] *mouhoti*, *Cyclemys dentata*, *Cuora amboinensis*, *C. galbinifrons*, *C. trifasciata*, *Geoemyda spengleri*, [*Geoemyda tchaponensis*, *Cyclemys dentata* in McDowell, 1964], *Heosemys* [*Geoemyda*] *depressa*, *Heosemys* [*Geoemyda*] *grandis*, *Malayemys* [*Damonia*] *subtrijuga*, *Hieremys annandalii*, *Siebenrockiella crassicollis*, *Sacalia bealei* [*Clemmys quadriocellata*], *Ocadia sinensis*, *Morenia ocellata*, *Mauremys mutica* [*Annamemys merklei*], *Kachuga trivittata*, *Batagur baska*, "*Geoclemys*" *palaeannamitica*); deBroin, 1970 (*Ptychogaster emydoides*, ventral view of poorly preserved specimens); Cagle, 1952 (*Graptemys barbouri**, *G. pulchra**); Carr, 1952 (palates and lower jaws* of *Graptemys* and *Malaclemys*); Deraniyagala, 1939 (*Melanochelys trijuga*); Ernst and Barbour, 1972 (*Clemmys guttata*, *C. muhlenbergii*, *C. insculpta*, *C. marmorata*, *Terrapene carolina*, *T. ornata*, *Malaclemys terrapin*, *Graptemys geographica*, *G. barbouri*, *G. pulchra*, *G. kohnii*, *G. pseudogeographica*, *G. flavimaculata*, *G. nigrinoda*, *Chrysemys picta*, *C. scripta*, *C. concinna*, *C. floridana*, *C. rubriventris*, *C. nelsoni*, *C. alabamensis*, *Deirochelys reticularis*, *Emydoidea blandingii*, photographs of variable quality, sutures usually indistinct); Fang, 1934 (*Clemmys* [*Chinemys*] *nigricans*, *Chinemys megaloccephala*, *C. reevesi*; all repeated in Wermuth and Mertens, 1961); Feuer, 1970 (*Emydoidea blandingii*, dor-

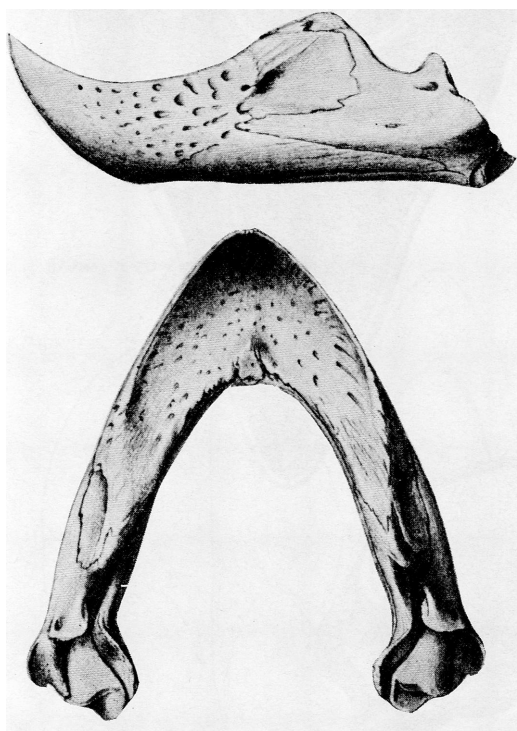


FIG. 211. *Lepidochelys kempii*, Cheloniidae. Lower jaw. Modified from Hay (1908a). See also Hay (1908b) and Carr (1952) for other cheloniid lower jaw figures.

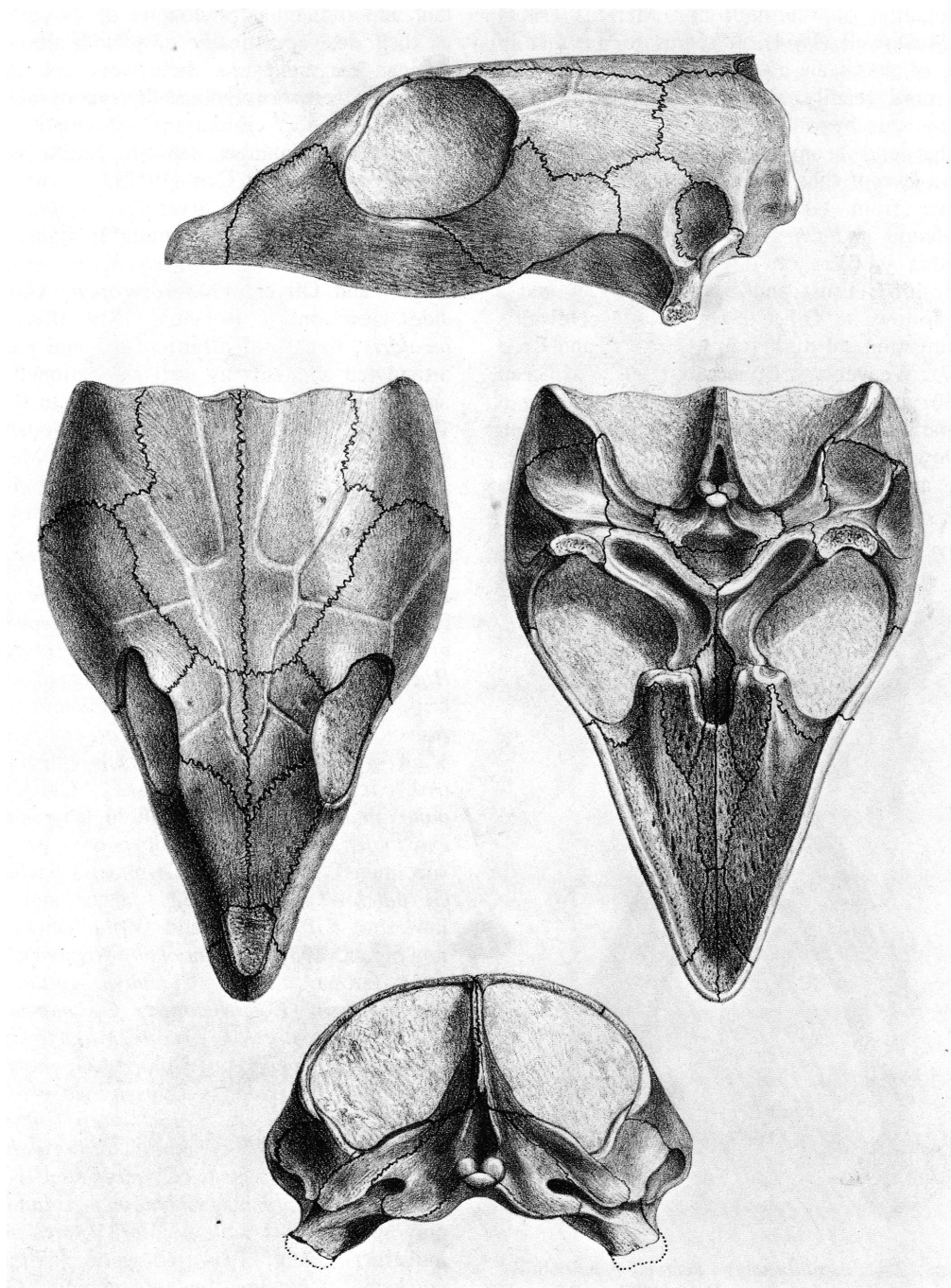
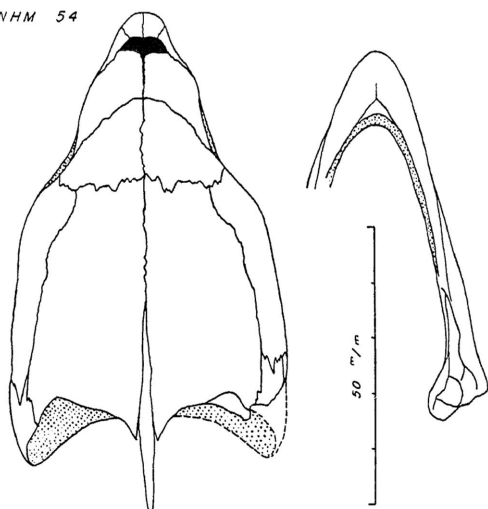


FIG. 212. *Puppigerus camperi* (type, missing and presumed lost; *fide* Moody, 1974), Cheloniidae, Eocene, England. From Owen and Bell (1849), with modifications from Moody (1974), *q.v.* for description and figures.

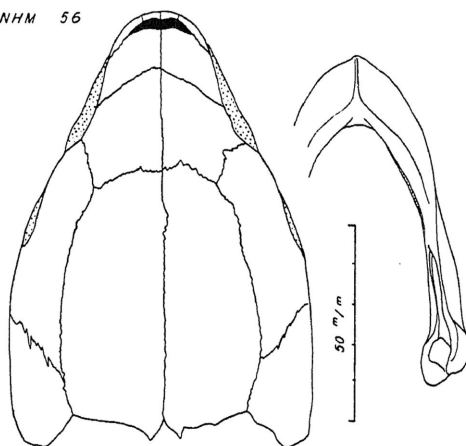
sal and lateral views only, figures crude and inaccurate); Fuchs, 1932 (*Emys orbicularis*, figure of embryo sectioned through processus pterygoideus externus); Gilmore, 1933 (*Chrysemys* [*Pseudemys*] *idahoensis**); Gray, 1855

(*Kachuga* [*Batagur*] *dhongoka*, *Chrysemys terapen* [*Emys decussata*], the skull labeled "*Emys subtrijuga*" is not *Malayemys subtrijuga*, and I do not know what is the best generic assignment); Gray, 1869 (*Terrapene*

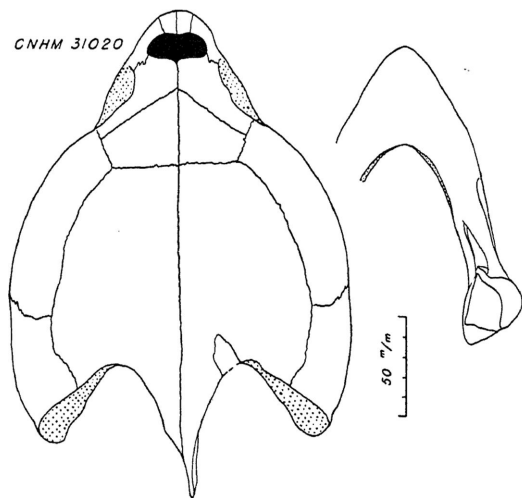
CNHM 54

*Eretmochelys imbricata*

CNHM 56

*Chelonia mydas*

CNHM 31020

*Caretta caretta*

Z 71

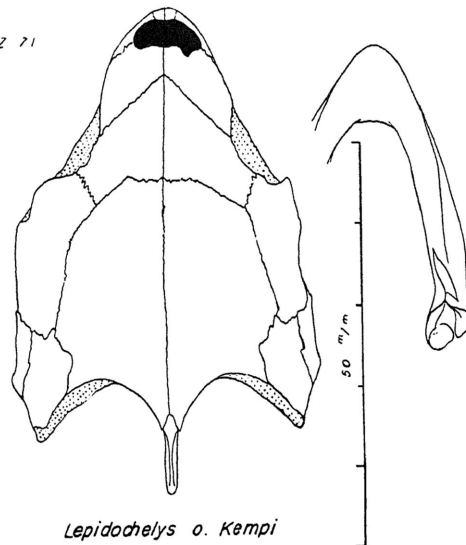
*Lepidochelys o. kempii*

FIG. 213. Dorsal views of the four Recent cheloniid genera. Dorsal views of lower jaws to right of each skull. From Zangerl (1958).

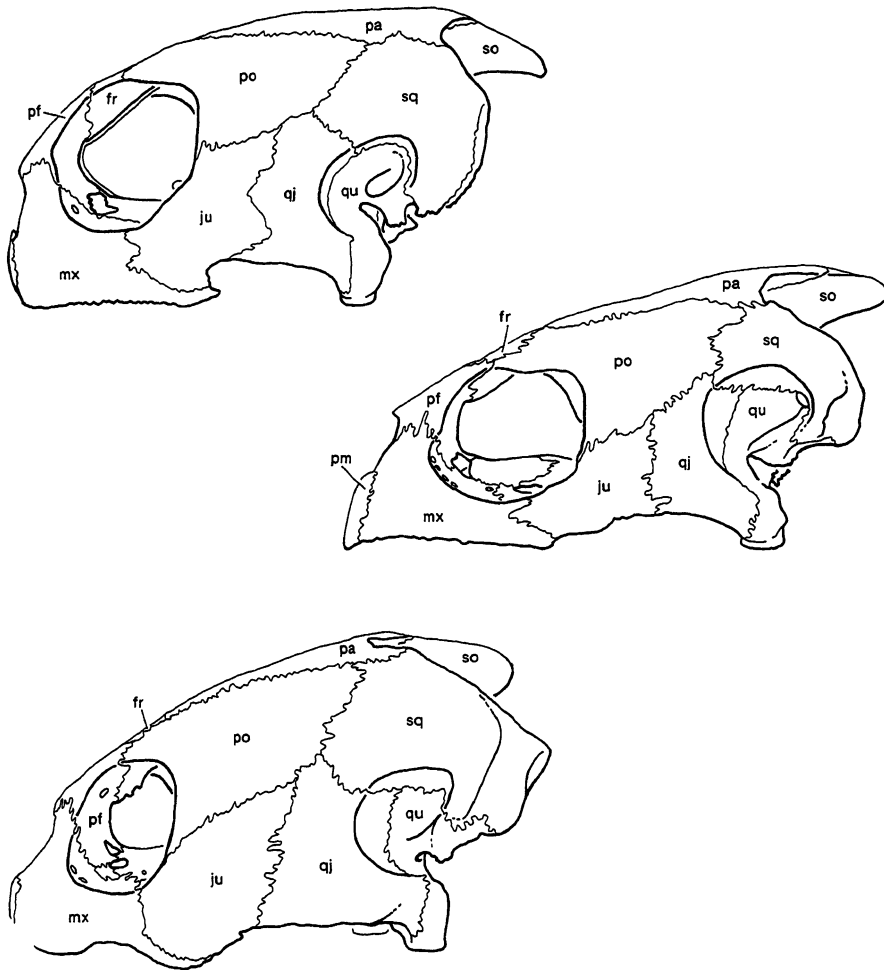


FIG. 214. Lateral views of Recent Cheloniidae. Upper. *Chelonia mydas* (AMNH 71597). Middle. *Eretmochelys imbricata* (AMNH 71598). Lower. *Caretta caretta* (AMNH 7163).

carolina [*Cistudo clausa*], *Cuora amboiensis*, *Melanochelys trijuga*, *Malayemys subtrijuga* [*Damonia macrocephala*], *Clemmys insculpta* [*Glyptemys pulchella*], *Siebenrockiella* [*Bellia*] *crassicolis*, *Batagur* [*Tetraonyx*] *baska*, *Kachuga trivittata* [*peguensis* and *trilineata*], *Hardella thurgi* [*Kachuga oldhami*], *Chrysemys scripta* [*Pseudemys serraia*, *Trachemys holbrookii*], *Malaclemys terrapin* [*concentrica*], all of these are repeated in Boulenger, 1889,

and Wermuth and Mertens, 1961; in the latter, figure 118, labeled *Pseudemys terrapen* is actually *Malaclemys terrapin*, whereas figure 93 is a redrawn version of the same figure); Gray, 1873b (*Ocadia sinensis*, repeated in Boulenger, 1889, and Wermuth and Mertens, 1961); Hay, 1908a (*Chrysemys* [*Trachemys*] *scripta*, dorsal and palatal views; *Echmatemys* sp.); Hoffmann, 1890 (*Mauremys* [*Clemmys*] *caspica*); Kunkel, 1912 (*Emys orbicularis* [*lutaria*], fully formed

chondrocranium, transverse sections through juvenile heads); Loveridge and Williams, 1957 (*Emys orbicularis*, *Mauremys* [*Clemmys*] *caspica*; anterior portion of palate, side view and anterior view of nose); McDowell, 1961 (*Grap-*

temys geographica, frontally sectioned skull showing cranial arteries and foramina); McDowell, 1964 (*Clemmys guttata*, *Mauremys caspica*, basicranium*, ear region*, lower jaws; *Hardella thurgii**, *Chrysemys alabamensis**,

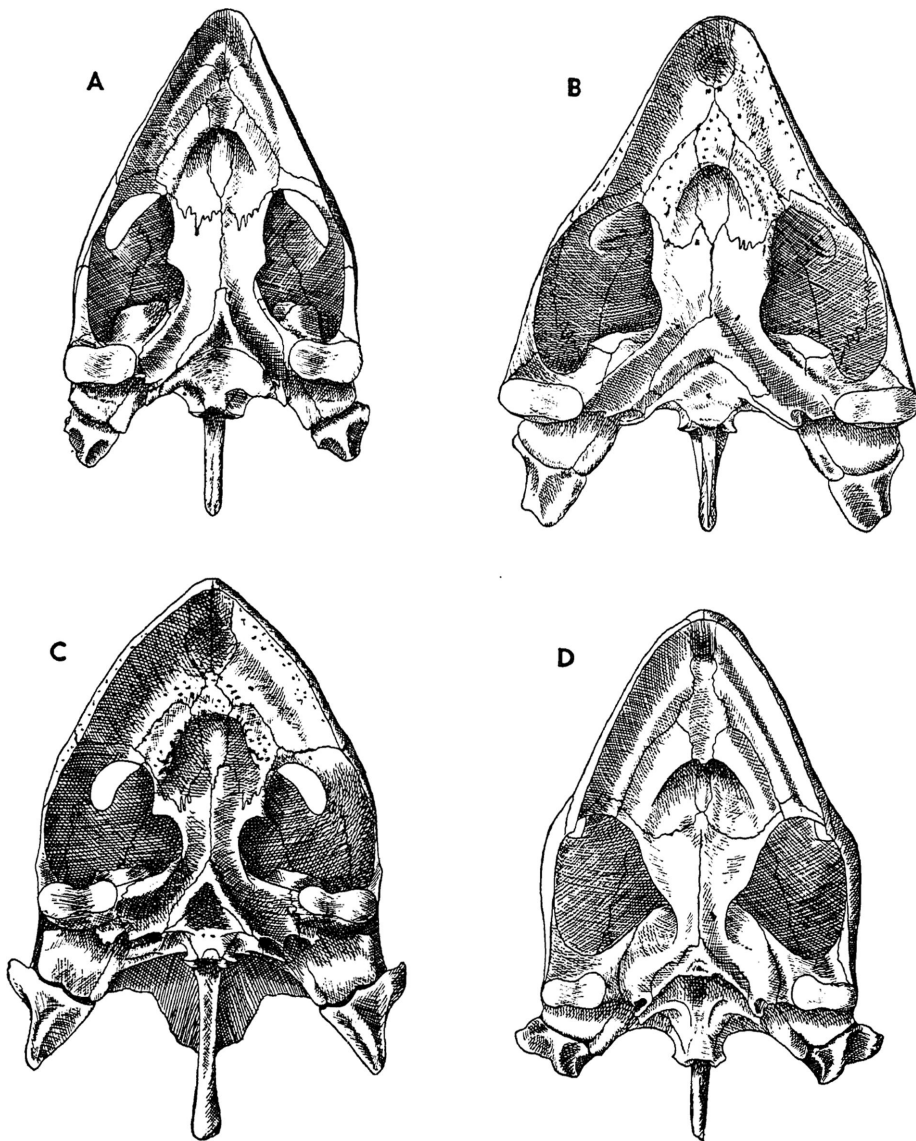


FIG. 215. Palatal views of the four Recent cheloniid genera. A. *Eretmochelys imbricata*. B. *Caretta caretta*. C. *Lepidochelys kempi*. D. *Chelonia mydas*. From Carr (1952) with permission of Comstock Press.

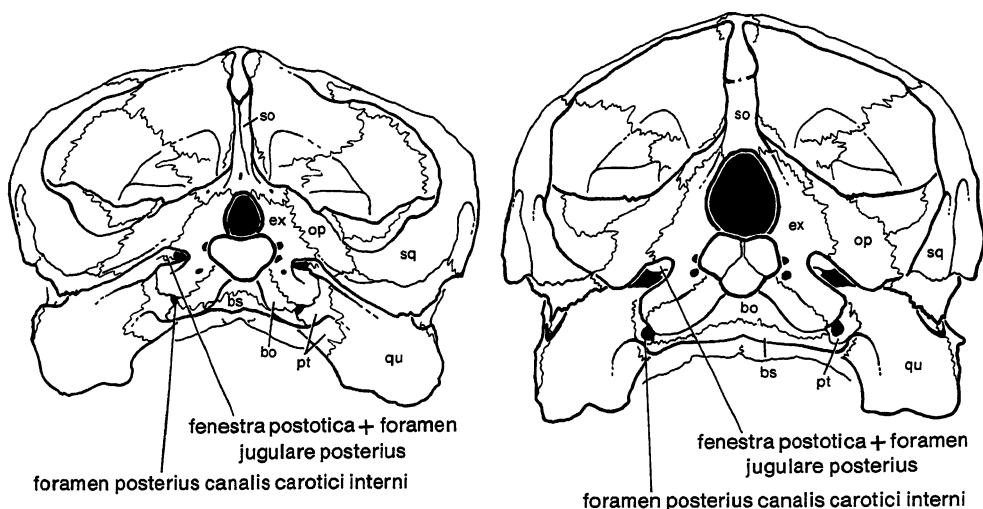


FIG. 216. Occipital views of Recent Cheloniidae. Left, *Caretta caretta* (AMNH 7163); right *Eretmochelys imbricata* (AMNH 71598).

TABLE 1
A Comparison of Species Distribution among Genera as Propounded in Two Classifications of the Emydidae

Wermuth and Mertens, 1961	McDowell, 1964
<i>Annamemys annamensis</i>	junior synonym of <i>Mauremys mutica</i>
<i>Batagur baska</i>	same
<i>Callagur borneoensis</i>	same
<i>Chinemys reevesi</i>	same
<i>Chinemys kwantungensis</i>	same
<i>Chinemys megalcephala</i>	(not mentioned)
<i>Chrysemys picta</i>	<i>Chrysemys (Chrysemys) picta</i>
<i>Clemmys bealei</i>	<i>Sacalia bealei</i>
<i>Clemmys caspica</i>	<i>Mauremys caspica</i>
<i>Clemmys guttata</i>	same
<i>Clemmys insculpta</i>	same
<i>Clemmys japonica</i>	<i>Mauremys japonica</i>
<i>Clemmys marmorata</i>	same
<i>Clemmys mühlenbergi</i>	same
<i>Clemmys nigricans</i>	not mentioned
<i>Cuora amboinensis</i>	same
<i>Cuora flavomarginata</i>	<i>Geoemyda flavomarginata</i>
<i>Cuora galbinifrons</i>	(not considered, see p. 270)
<i>Cuora trifasciata</i>	same
<i>Cuora yunnanensis</i>	same
<i>Cyclemys dentata</i>	same
<i>Cyclemys mouhotii</i>	<i>Geoemyda mouhotii</i>
<i>Deirochelys reticularia</i>	same
<i>Emys blandingii</i>	<i>Emydoidea blandingi</i>
<i>Emys orbicularis</i>	same

TABLE 1 — (Continued)

Wermuth and Mertens, 1961	McDowell, 1964
<i>Geoclemys hamiltonii</i>	same
<i>Geoemyda annulata</i>	<i>Rhinoclemys annulata</i>
<i>Geoemyda areolata</i>	<i>Rhinoclemys areolata</i>
<i>Geoemyda depressa</i>	<i>Heosemys depressa</i>
<i>Geoemyda funerea</i>	<i>Rhinoclemys funerea</i>
<i>Geoemyda grandis</i>	<i>Heosemys grandis</i>
<i>Geoemyda leytenis</i>	<i>Heosemys leytenis</i>
<i>Geoemyda pulcherrima</i>	<i>Rhinoclemys pulcherrima</i>
<i>Geoemyda punctularia</i>	<i>Rhinoclemys punctularia</i>
<i>Geoemyda rubida</i>	<i>Rhinoclemys rubida</i>
<i>Geoemyda silvatica</i>	<i>Heosemys silvatica</i>
<i>Geoemyda spengleri</i>	same
<i>Geoemyda spinosa</i>	<i>Heosemys spinosa</i>
<i>Geoemyda tcheponensis</i>	<i>Cyclemys dentata</i>
<i>Geoemyda tricarinata</i>	<i>Melanochelys tricarinata</i>
<i>Geoemyda trijuga</i>	<i>Melanochelys trijuga</i>
<i>Graptemys barbouri</i>	<i>Malaclemys barbouri</i>
<i>Graptemys geographica</i>	<i>Malaclemys geographica</i>
<i>Graptemys kohnii</i>	<i>Malaclemys kohni</i>
<i>Graptemys oculifera</i>	<i>Malaclemys oculifera</i>
<i>Graptemys pseudogeographica</i>	<i>Malaclemys pseudogeographica</i>
<i>Graptemys pulchra</i>	<i>Malaclemys pulchra</i>
<i>Hardella thurgii</i>	<i>Hardella thurgii</i> and <i>Hardella indi</i>
<i>Hieremys annandali</i>	same
<i>Kachuga dhongoka</i>	same
<i>Kachuga kachuga</i>	same
<i>Kachuga smithii</i>	same
<i>Kachuga sylhetensis</i>	same
<i>Kachuga tecta</i>	same
<i>Kachuga trivittata</i>	same
<i>Malaclemys terrapin</i>	same
<i>Malayemys subtrijuga</i>	same
<i>Morenia ocellata</i>	same
<i>Morenia petersi</i>	same
<i>Notochelys platynota</i>	same
<i>Ocadia sinensis</i>	same
<i>Orlitia borneensis</i>	same
<i>Pseudemys concinna</i>	<i>Chrysemys (Pseudemys) concinna</i>
<i>Pseudemys dorbigni</i>	<i>Chrysemys (Trachemys) dorbigni</i>
<i>Pseudemys floridana</i>	<i>Chrysemys (Pseudemys) floridana</i>
<i>Pseudemys grayi</i>	?
<i>Pseudemys ornata</i>	?
<i>Pseudemys rubiventris</i>	<i>Chrysemys (Pseudemys) rubiventris</i>
<i>Pseudemys scripta</i>	<i>Chrysemys (Trachemys) scripta</i>
<i>Pseudemys terrapen</i>	<i>Chrysemys (Trachemys) terrapen</i>
<i>Siebenrockiella crassicollis</i>	same
<i>Terrapene carolina</i>	same
<i>Terrapene coahuila</i>	same
<i>Terrapene klauberi</i>	(status to be determined)
<i>Terrapene mexicana</i>	same
<i>Terrapene nelsoni</i>	(status to be determined)
<i>Terrapene ornata</i>	same

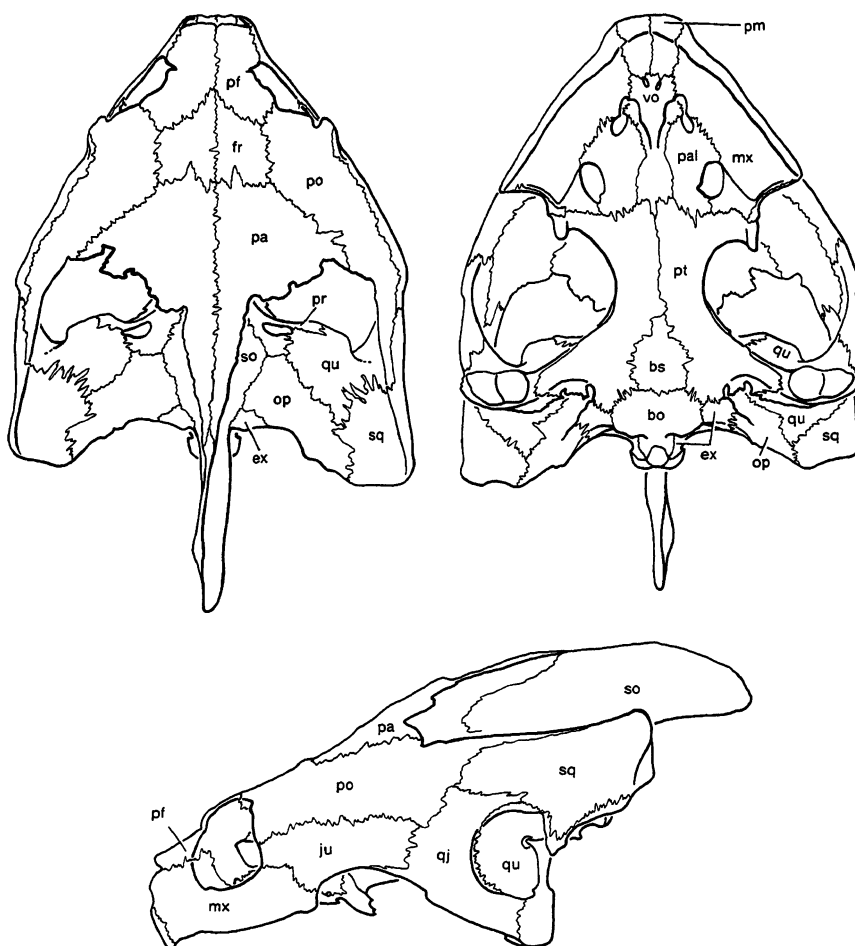


FIG. 217. *Chelydra serpentina* (AMNH 5305; 97 mm.), Chelydridae, no data. From Gaffney (1975e).

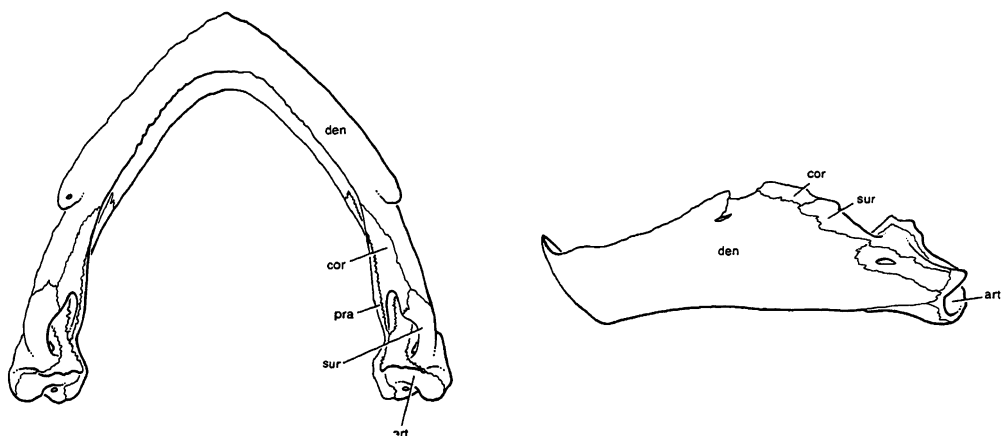


FIG. 218. *Chelydra serpentina* (AMNH 5305), Chelydridae, no data. Lower jaw in dorsal (left) and lateral (right) views. From Gaffney (1975e).

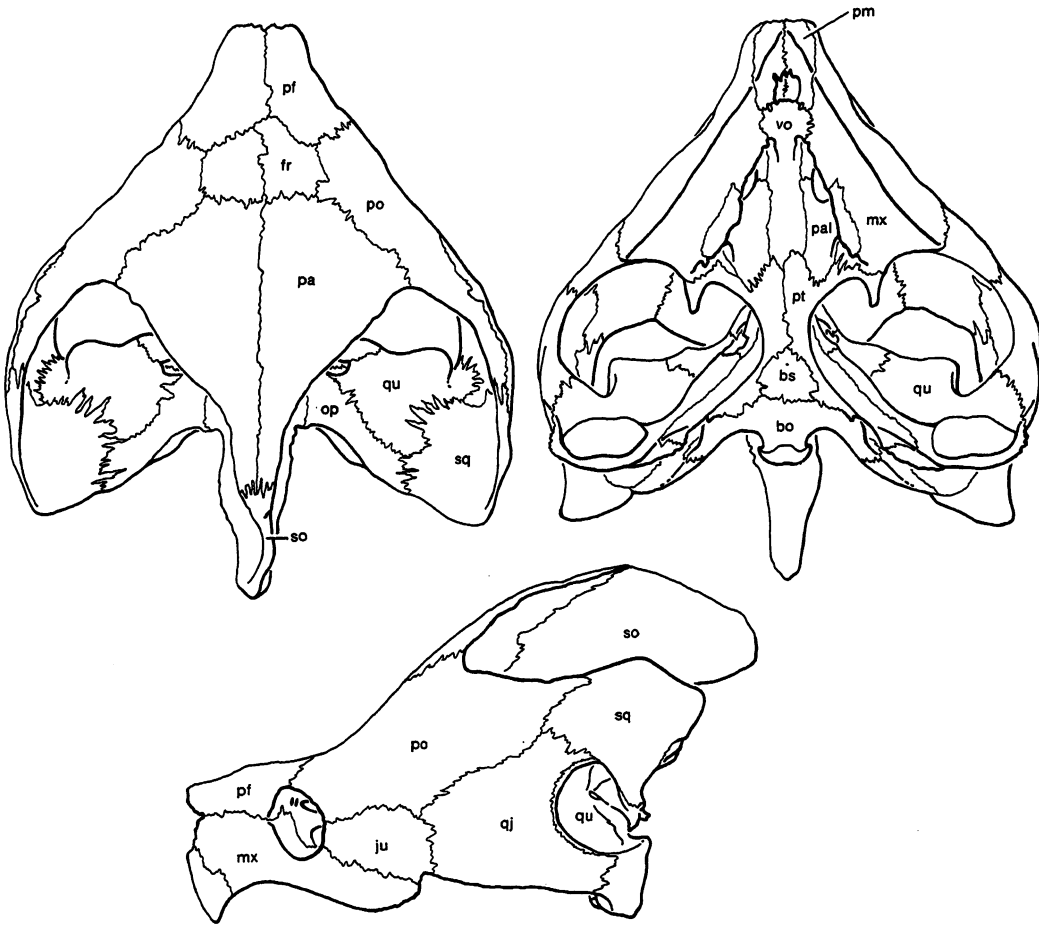


FIG. 219. *Macroclemys temminckii* (AMNH 58251; 179 mm.), Chelydridae, no data. From Gaffney (1975e).

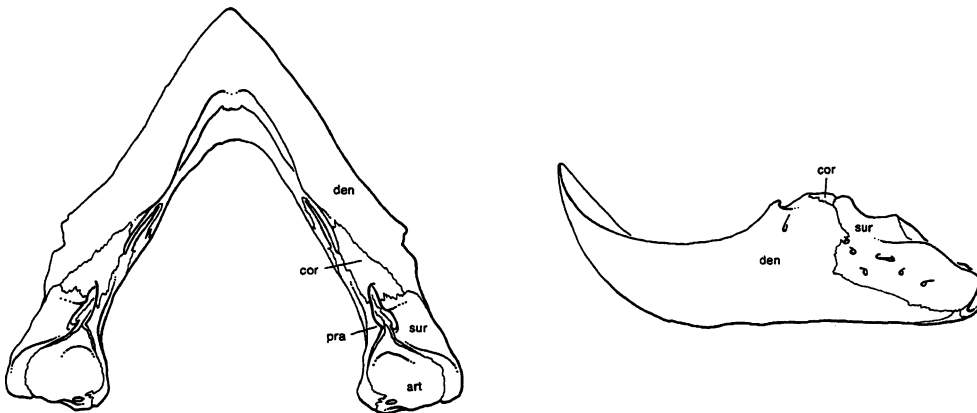


FIG. 220. *Macroclemys temminckii* (AMNH 58251), Chelydridae, no data. Lower jaw in dorsal (left) and lateral (right) views. From Gaffney (1975e).

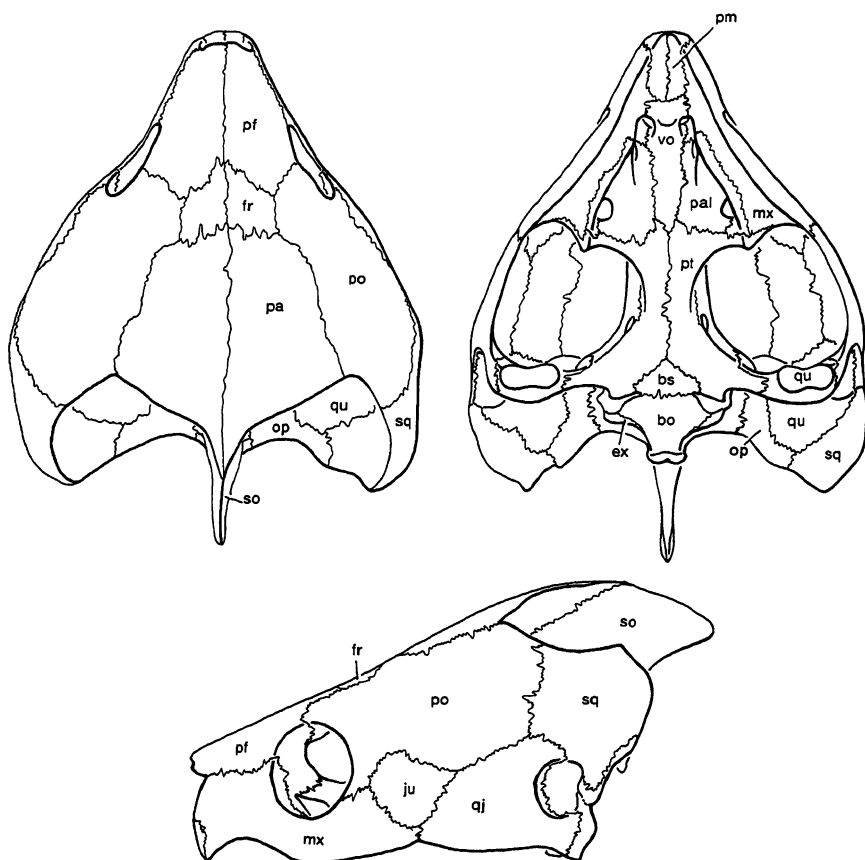


FIG. 221. *Platysternon megacephalum* (AMNH 92740; 42 mm.), Chelydridae, no data. From Gaffney (1975e).

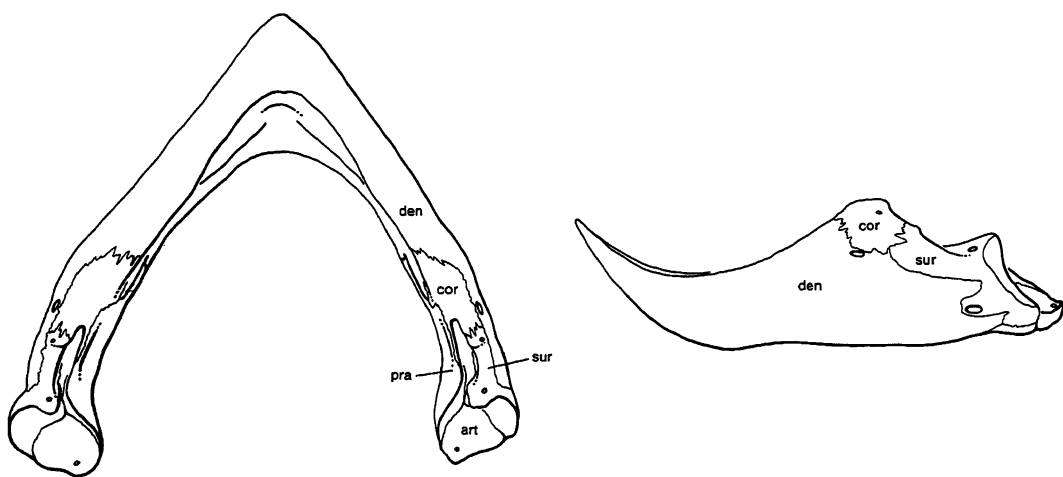


FIG. 222. *Platysternon megacephalum* (AMNH 92740), Chelydridae, no data. Lower jaw in dorsal (left) and lateral (right) views. From Gaffney (1975e).

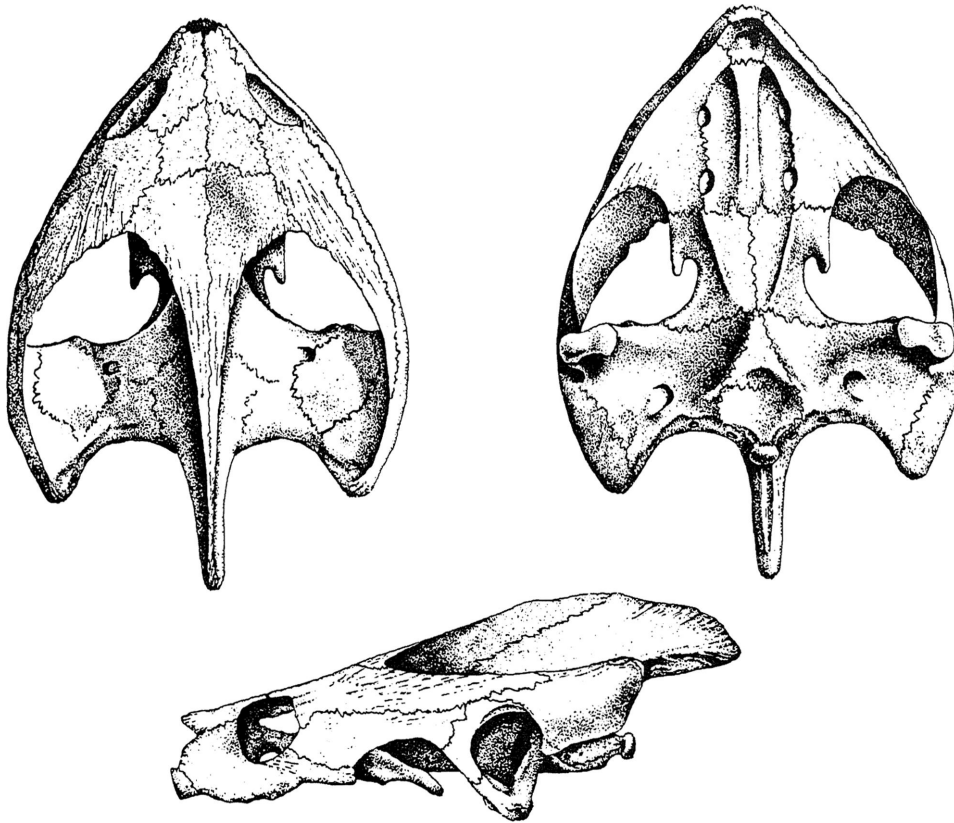


FIG. 223. *Protochelydra zangerli* (SMM P72.34.20; 78 mm.), Chelydridae, Tongue River Formation, Paleocene, Wannagan Creek Quarry, Billings County, North Dakota. Restored views from Erickson (1973), posterior limits of pterygoid doubtful as figured.

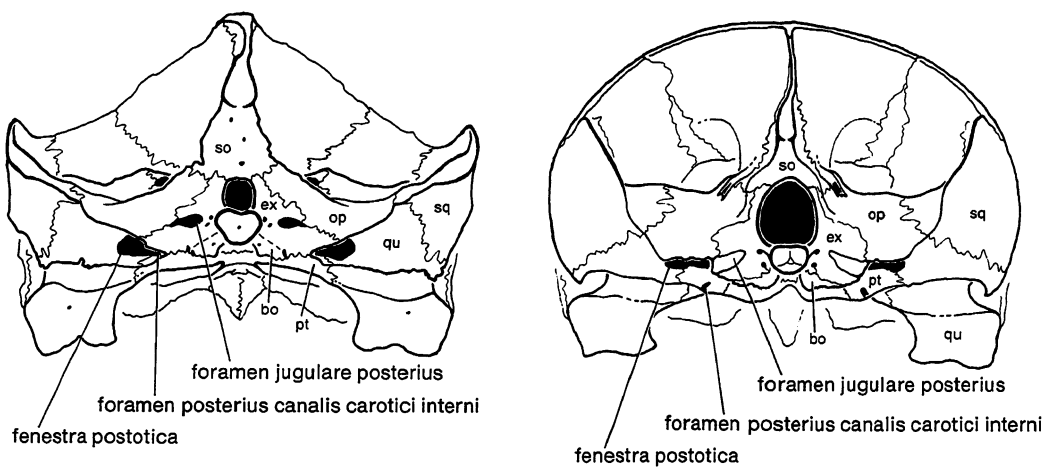


FIG. 224. Occipital views of Recent Chelydridae. Left, *Macroclemys temminckii* (AMNH 58251); right, *Platysternon megacephalum* (AMNH 92740). The foramen jugulare posterius in *Platysternon* is usually closed off from the fenestra postotica but in this specimen, which is apparently a juvenile, the foramen is open laterally.

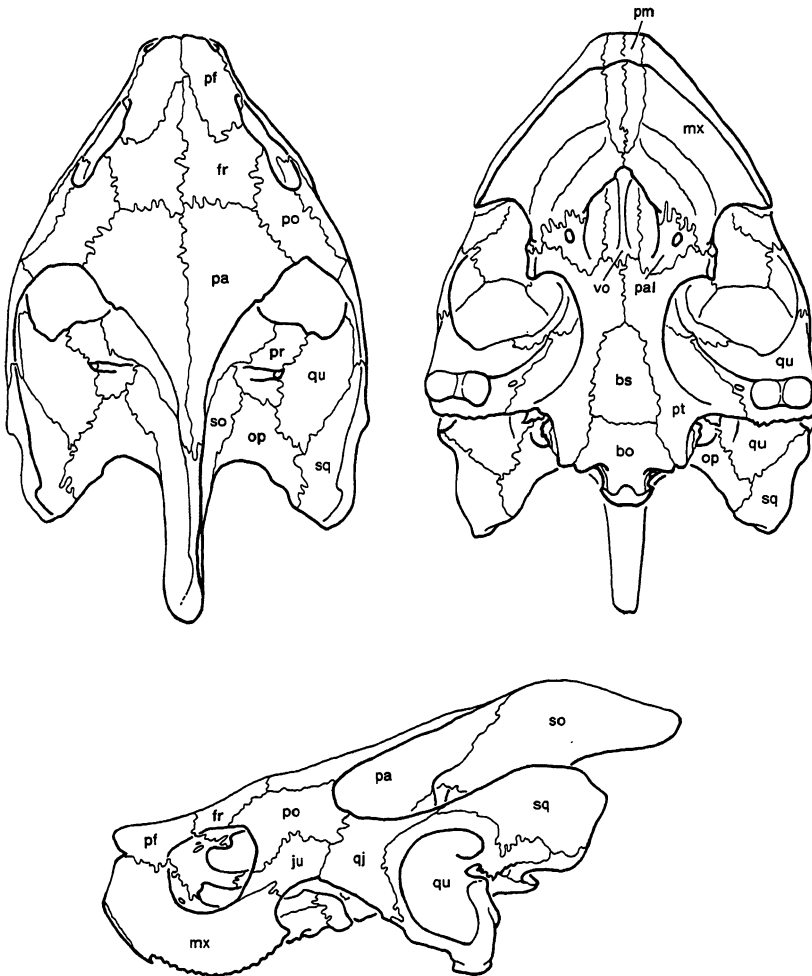


FIG. 225. *Batagur baska* (NMNH 29483; 93 mm.), Emydidae, Indragiri River, Sumatra.

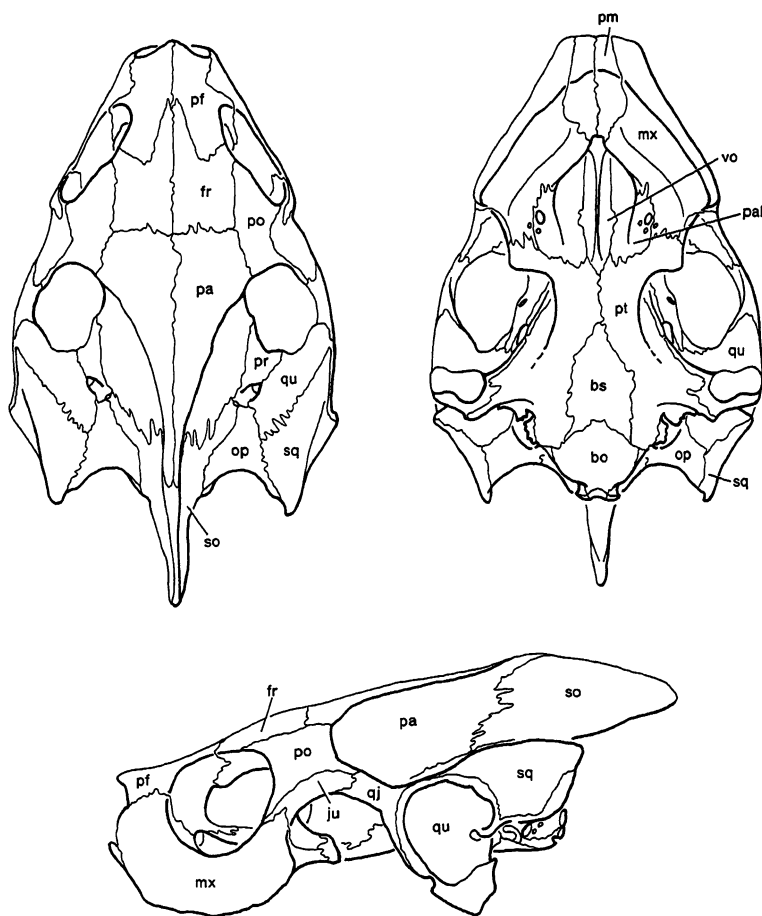


FIG. 226. *Callagur borneoensis* (AMNH 80933; 50 mm.), Emydidae, Kuching, Sarawak, Federation of Malaysia.

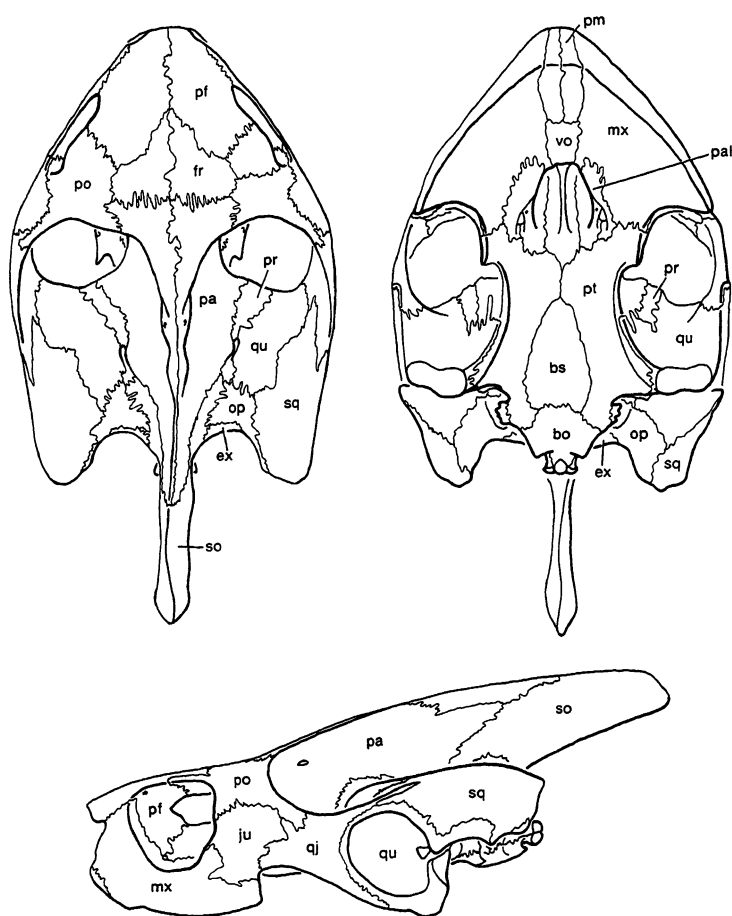


FIG. 227. *Chinemys reevesi* (AMNH 31117; 42 mm.), Emydidae, Ningkwo, Anhwei Province, Peoples' Republic of China. The right postorbital is divided by an anomalous suture.

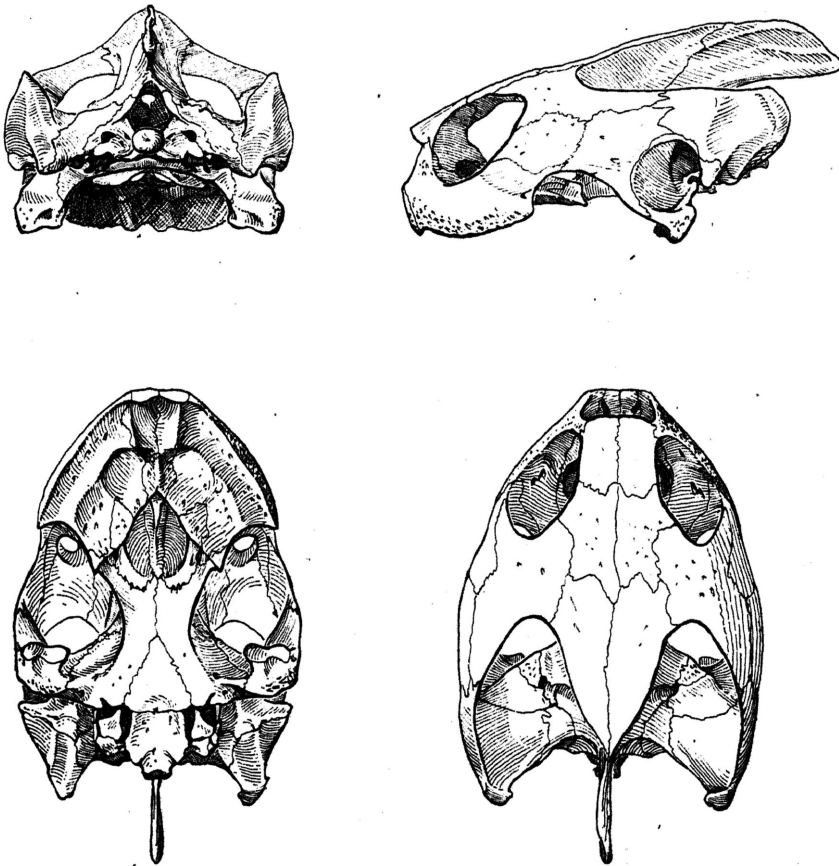


FIG. 228. *Chrysemys (Pseudemys) alabamensis*, Emydidae. From McDowell (1964).

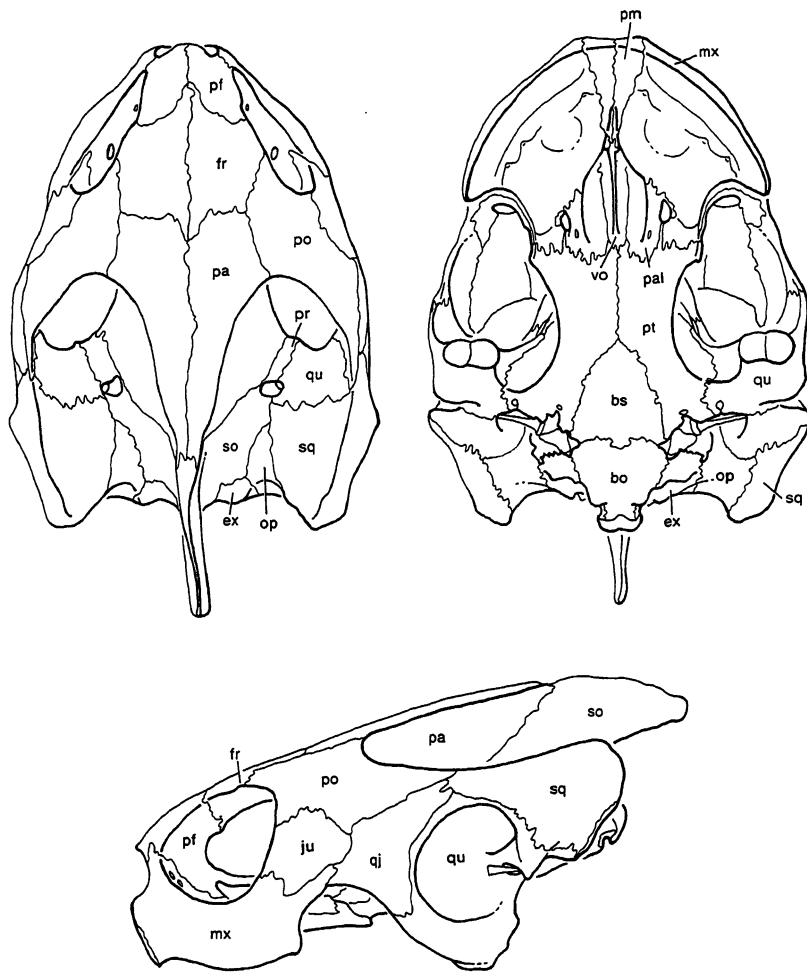


FIG. 229. *Chrysemys (Pseudemys) concinna* (AMNH 111960; 44 mm.), Emydidae, Colorado River, Travis County, Texas.

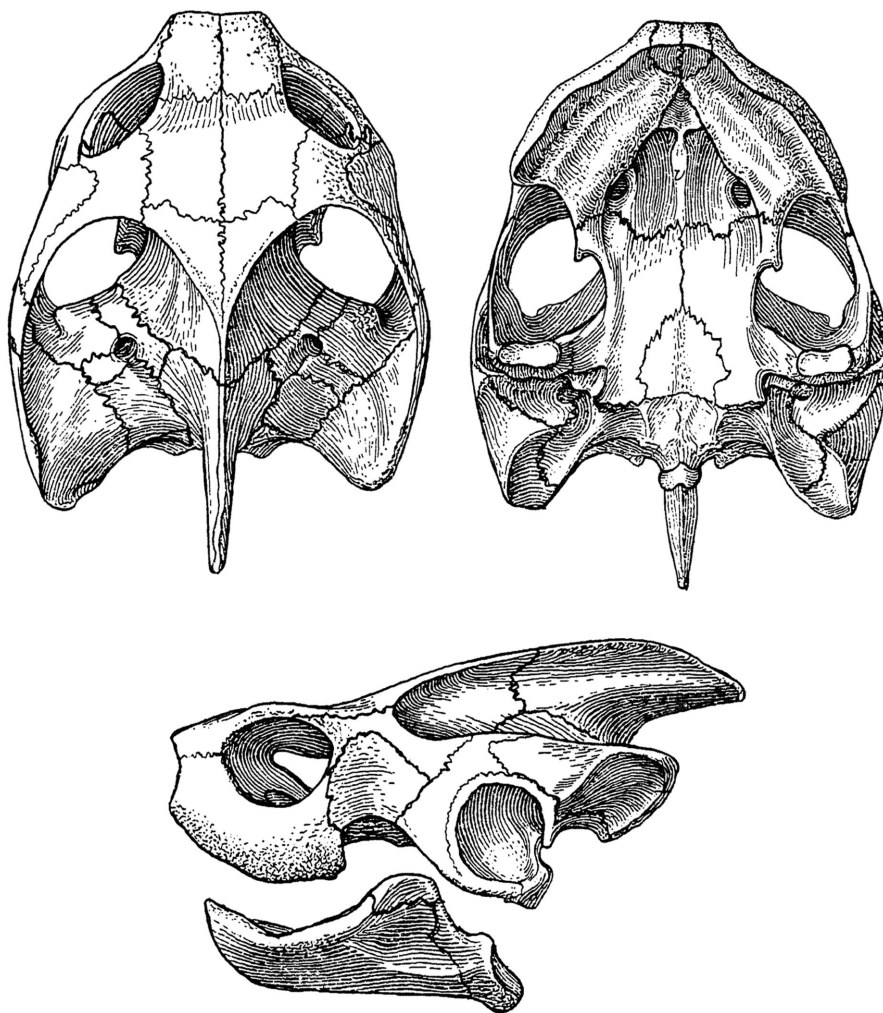


FIG. 230. *Chrysemys* (subgenus indet.) *idahoensis* (NMNH 12059; 57 mm.), Emydidae, Hagerman Lake beds, Pliocene, *Plesippus* Quarry, near Hagerman, Twin Falls County, Idaho. Modified from Gilmore (1933), who referred it to *Pseudemys*.

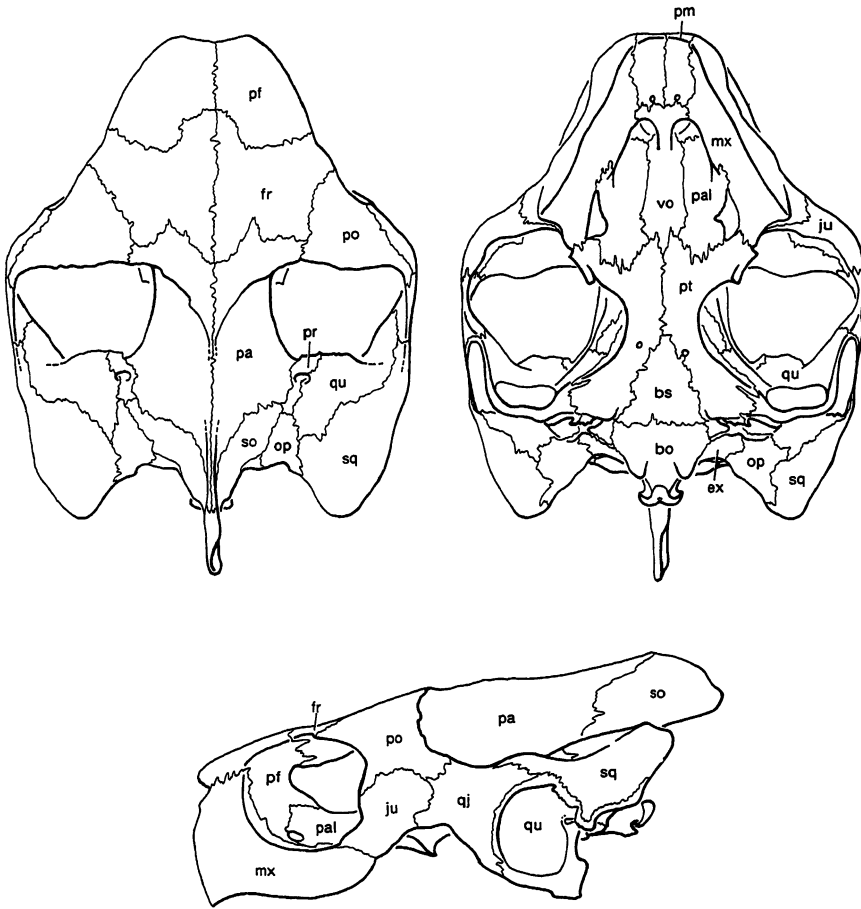


FIG. 231. *Clemmys insculpta* (AMNH 69793; 43 mm.), Emydidae, Ithaca, Tompkins County, New York.

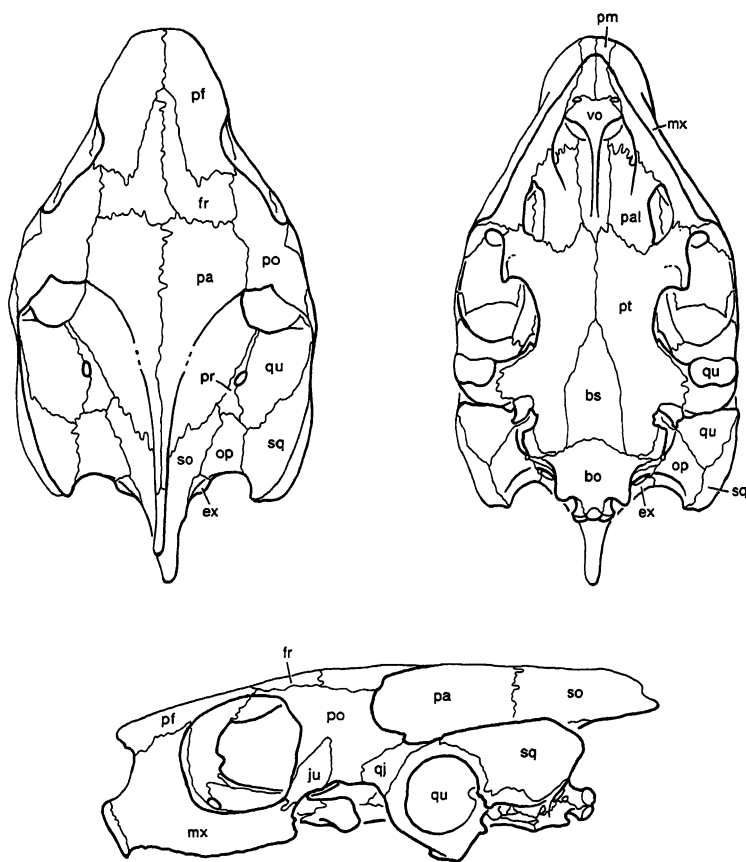


FIG. 232. *Cuora trifasciata* (AMNH 30147; 30 mm.), Emydidae, Nodda, Hainan Island, Kwangtung Province, Peoples' Republic of China.

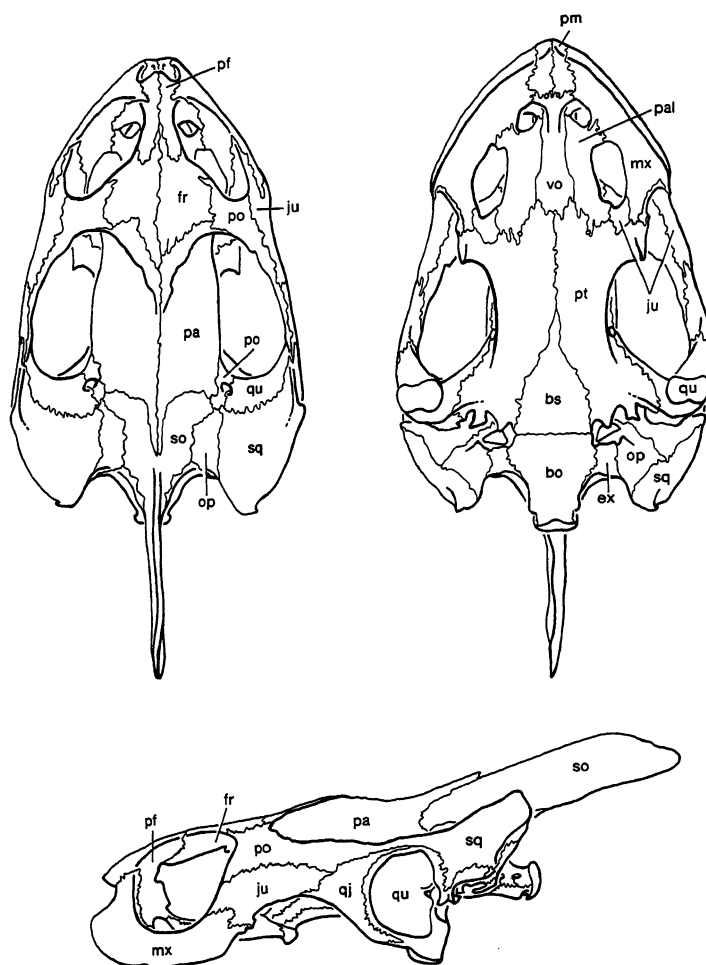


FIG. 233. *Deirochelys reticularia* (AMNH 73810; 45 mm.), Emydidae, Silver Springs, Marion County, Florida.

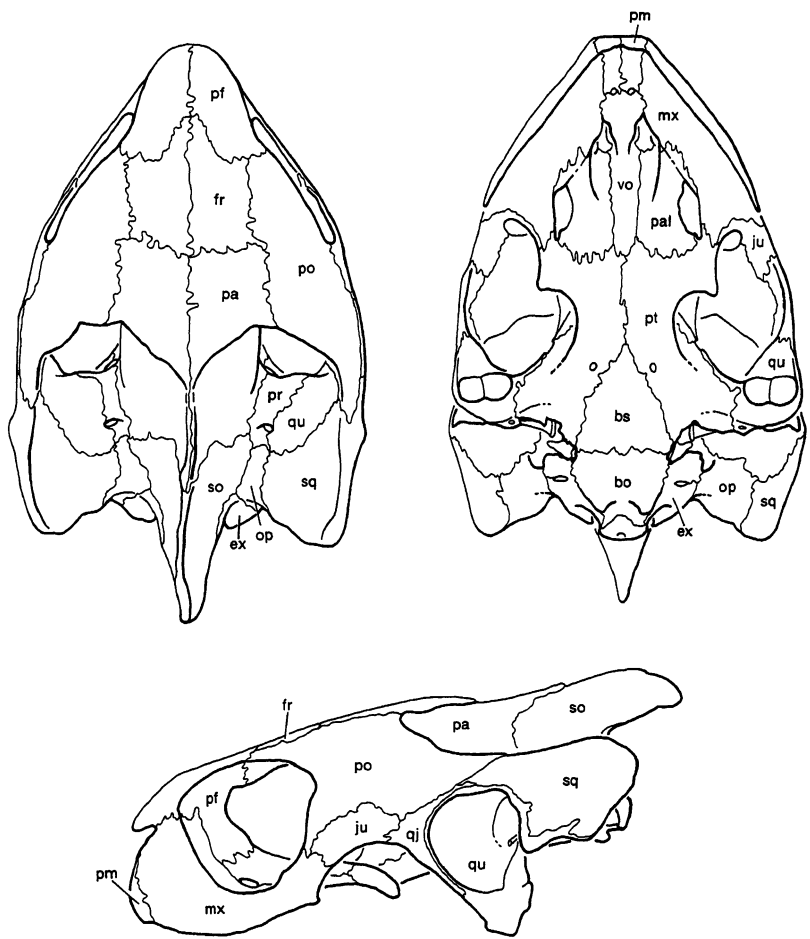


FIG. 234. *Emys orbicularis* (MCZ 31976; 35 mm.), Emydidae, Dalmatia.

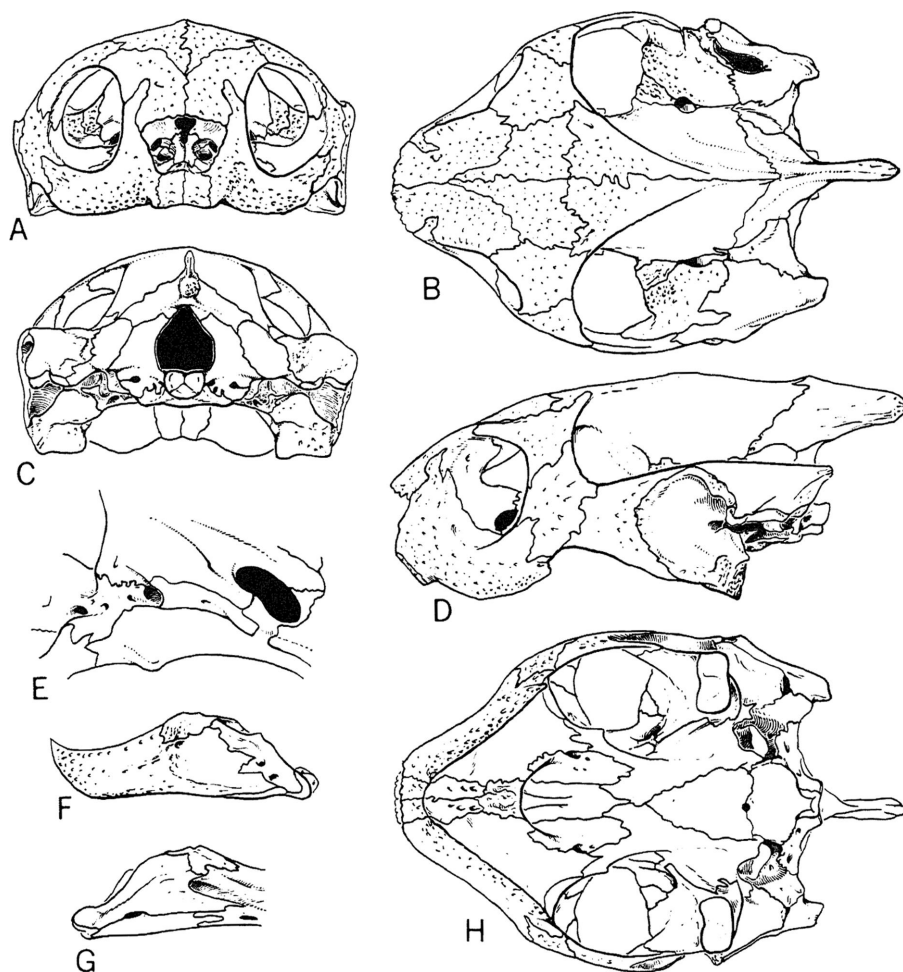


FIG. 235. *Geoclemys hamiltoni*, Emydidae. A. Anterior; B. dorsal; C. Occipital; D. Lateral; E. left ethmoid region; F. Lateral view of lower jaw; G. Medial view of left lower jaw ramus; H. Palatal. From McDowell (1964).

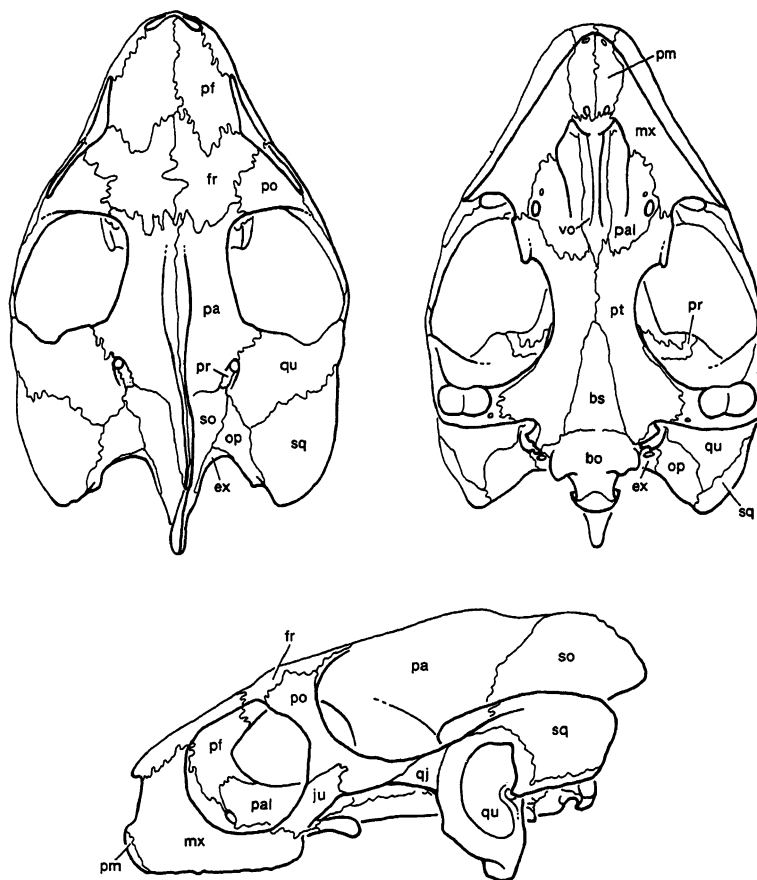


FIG. 236. *Geoemyda* (*Cyclemys* of Wermuth and Mertens, 1961) *mouhotii* (AMNH 28336; 41 mm.), Emydidae, Nodda, Hainan Island, Kwangtung Province, Peoples' Republic of China.

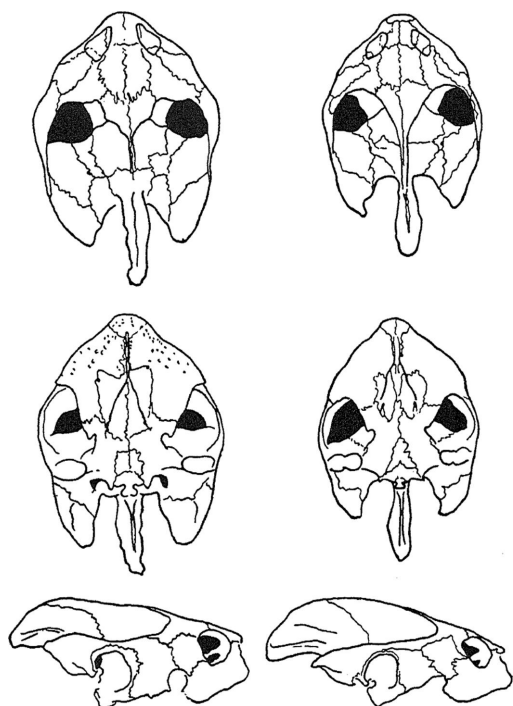


FIG. 237. *Graptemys barbouri* (left, Chipola River, Florida) and *Graptemys pulchra* (right, Tulane Univ. 13472, Escambia River, Florida), Emydidae. From Cagle (1952). Both skulls are presumed females, see Ernst and Barbour (1972) for figures of males.

*Geoclemys hamiltoni**, *Orlitia borneensis*, *Siebenrockiella crassicolis**); Milstead, 1969 (low quality lateral view photographs of *Terrapene carolina*, *T. ornata*, and *T. nelsoni*); Ruckes, 1937a (side views only of *Chrysemys* sp., *Heosemys* sp., *Geoemyda* sp., *Cyclemys* sp.); Schwarz, 1934 (*Chrysemys* [*Pseudemys*] *scripta*, *Chinemys* [*Geoclemys*] *reevesii*, figures of embryos sectioned through processus pterygoideus externus); Shiino, 1913 (cranial nerves and brain of *Clemmys* [*Nanemys*] *gut-tata*); Shindo, 1914 (*Emys orbicularis* [*europaea*], cranial arteries and transverse section); Siebenrock, 1897 (*Cyclemys dentata* [*dhor*], *Heosemys* [*Geoemyda*] *spinosa*, sagittal sections; *Rhinoclemys* [*Nicoria*] *punctularia**, *Emys orbicularis**, *Chrysemys ornata*, inner

views of ear elements; *Rhinoclemys* [*Nicoria*] *punctularia*, oblique view of ear, *Mauremys* [*Clemmys*] *caspica*, *Cuora* [*Cyclemys*] *amboinensis*, *Chrysemys ornata*, dorsal views of pterygoids); Smith, 1931 (*Hieremys annandalei*, *Malayemys* [*Damonia*] *subtrijuga*); Taylor, 1895 (side views of *Terrapene* species); Wegner, 1959 (*Orlitia borneensis*, good half-tones of ethmoid region and lateral view).

FAMILY TESTUDINIDAE (FIGS. 258-267): There are no detailed studies of testudinid cranial morphology and Siebenrock (1897) stands as the only effort to figure recent testudinid basicrania. Bramble (1971) partially rectified this by describing *Gopherus* and its near relatives. Testudinid skulls are figured in Gray (1855), Gunther (1877) and Loveridge and Williams (1957). Thomson (1932) has a limited description with poor figures of *Testudo graeca*.

I am using the classification published by Auffenberg (1974) and essentially developed from Loveridge and Williams (1957). Auffenberg provided data on fossil forms but also listed all Recent species with references. When used in combination with Wermuth and Mertens (1961 and 1977) it is extremely useful as an introduction to the literature. The most important systematic paper on testudinids is Loveridge and Williams (1957) who review the African testudinids (the region of greatest generic diversity) and present a phylogeny and discussion of relationships within the family. See also Williams (1950b and 1952a).

Anderson, 1872 (*Geochelone emys* [*Testudo phayrei*], side view only); Auffenberg, 1963 (*Geochelone incisa*); Bogert and Oliver, 1945 (*Gopherus agassizii*, *G. berlandieri*, *G. polyphemus*; anterior views of palates retaining corneous beak on feeding surfaces); Boulenger, 1889 (*Kinixys erosa*); Bourret, 1941 (*Geochelone* [*Testudo*] *elongata*, *G. [T.] emys*, *G. [T.] impressa*; *G. elongata* is redrawn in Wermuth and Mertens, 1961); Case, 1925 (*Stylomys nebrascensis*); Deraniyagala, 1939 (*Geochelone* [*Testudo*] *elegans*, redrawn in Wermuth and Mertens, 1961); Ernst and Barbour, 1972 (*Gopherus agassizii*, *G. berlandieri*, *G. poly-*

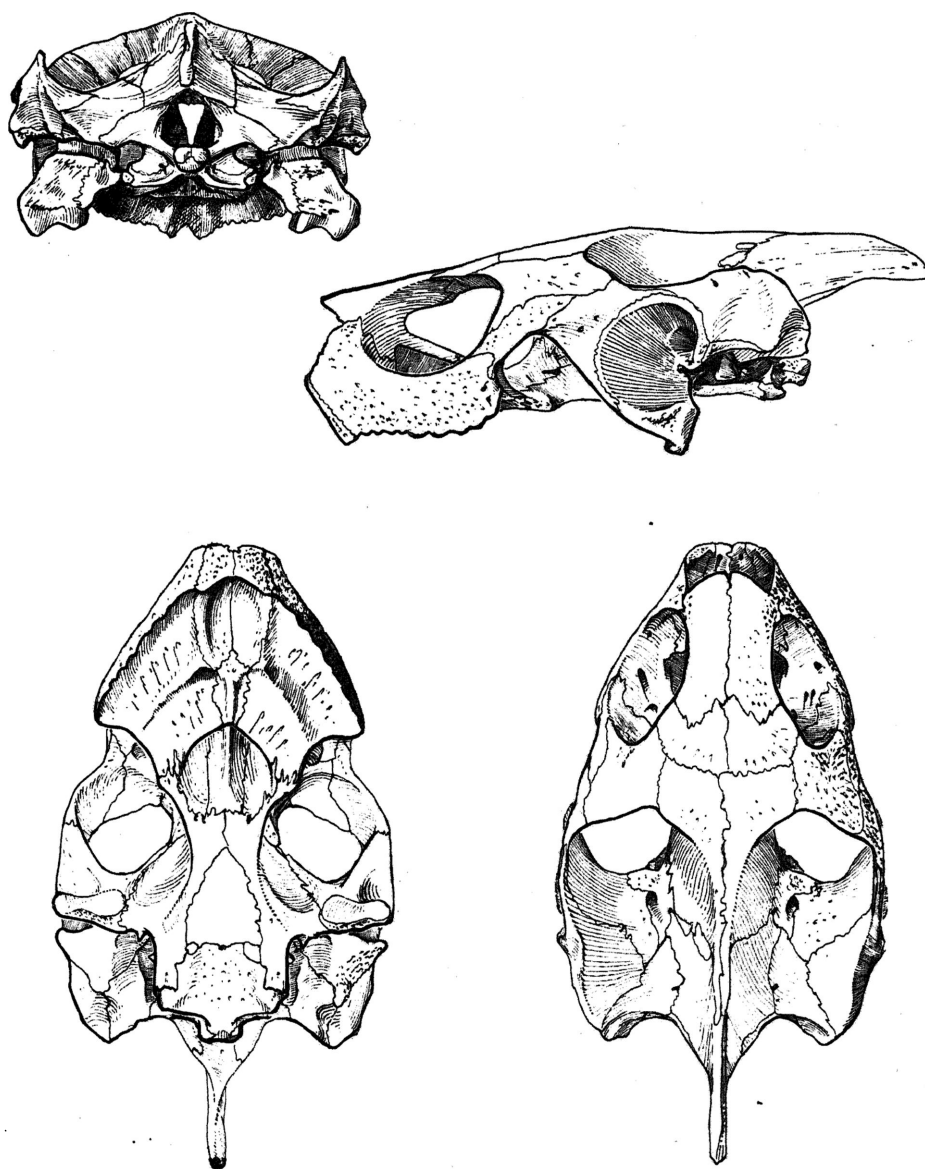


FIG. 238. *Hardella thurgii*, Emydidae. From McDowell (1964).

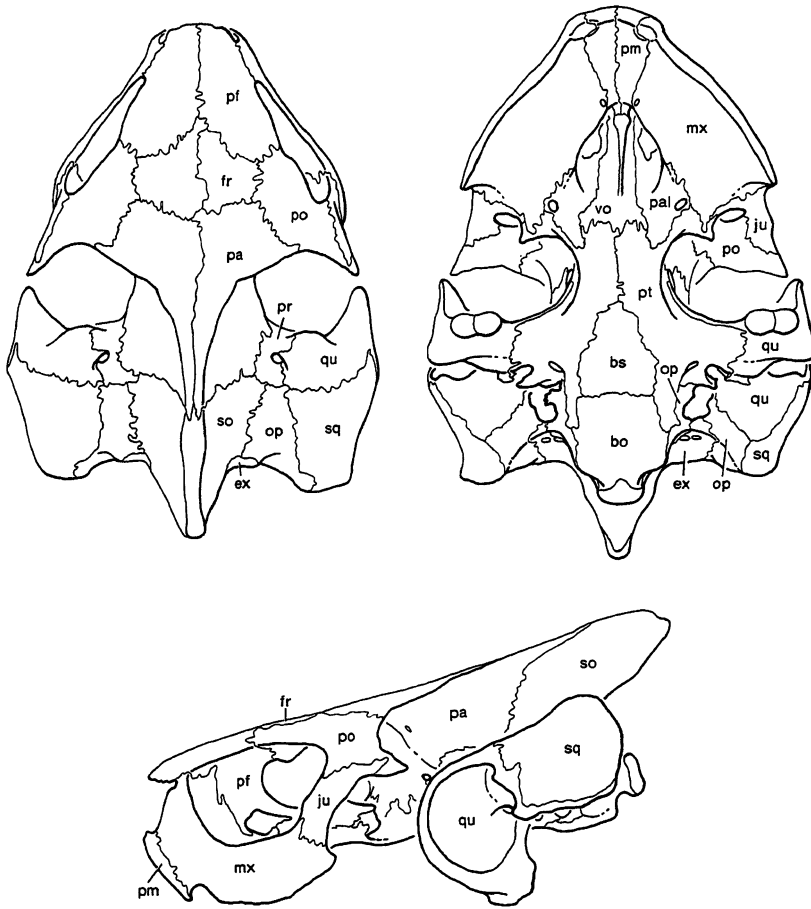


FIG. 239. *Hieremys annandalii* (AMNH 16213; 67 mm.), Emydidae, Paknum Chao Proya, Thailand.

phemus; photographs of variable quality, sutures usually indistinct); Gilbert, 1898 (*Geochelone gilberti* [*Xerobates undata*]); Gilmore, 1946 (*Gopherus* [*Testudo*] *preextans*); Gray, 1855 (*Geochelone elephantopus* [*Testudo planiceps*], *Geochelone* [*Testudo*] *indica*, *G. denticulata* [*Testudo tabulata*]; *G. elephantopus* is repeated in Wermuth and Mertens, 1961); Gray, 1869 (*Geochelone emys* [*Testudo falconeri*] repeated in Boulenger, 1889, and Wermuth and Mertens, 1961; *Geochelone elongata* [*Peltastes elongatus*]); Gray, 1873e (*Gopherus polyphemus* [*Xerobates gopher*],

Geochelone [*Asterochelys*] *radiata*, *Geochelone denticulata* [*Chelonoidis tabulata*], *Testudo* [*Chersinella*] *graeca*, *Homopus areolatus*, *Chersina angulata*, *Pyxis arachnoides*, *Kinixys erosa*; palates and lower jaws only, no sutures, otherwise good halftones); Gunther, 1877 (*Geochelone gigantea* [*Testudo elephantica*, *T. ponderosa*], *Geochelone* [*T.*] *vosmaeri*, *G.* [*T.*] *grayi* [*inepta* and *triserrata*], *G.* [*T.*] *elephantopus** [*microphyes*, *ephippium*, *nigrita*, *abingdonii*]; high quality halftones); Hay, 1908a (*Stylemys nebrascensis*, *Geochelone* [*Testudo*] *osborniana*, *G.* [*T.*] *impensa*, *G.* [*T.*]

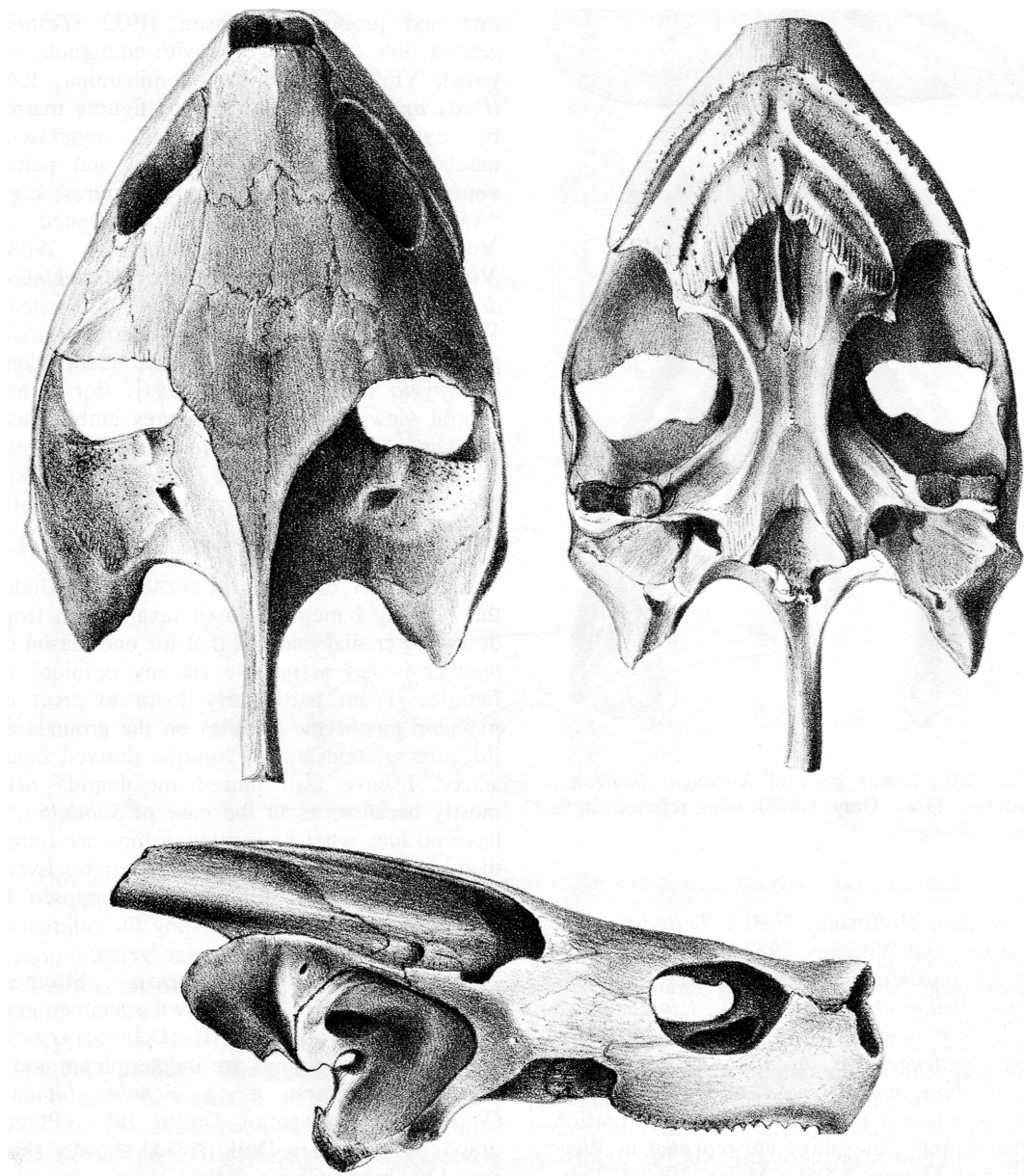


FIG. 240. *Kachuga dhongoka*, Emydidae. From Gray (1855) who referred it to *Batagur dhongoka*.

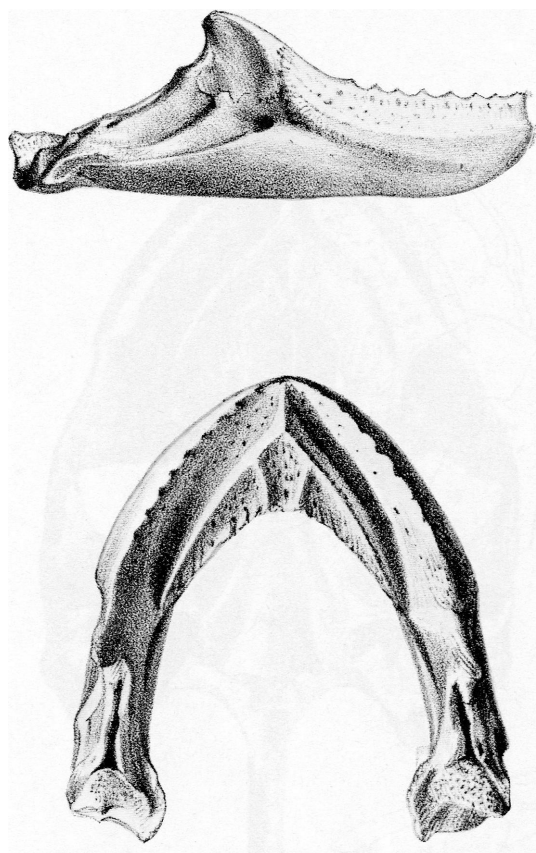


FIG. 241. Lower jaws of *Kachuga dhongoka*, Emydidae. From Gray (1855) who referred it to *Batagur dhongoka*.

orthopygia); Hoffmann, 1890 ("Testudo" sp.); Loveridge and Williams, 1957 (*Geochelone sulcata*, *G. pardalis**, *Testudo graeca**, *T. kleinmanni*, *Malacochersus tornieri*, *Psammobates oculifer**, *P. tentorius*, *Chersina angulata*, *Homopus boulengeri*, *H. areolatus*, *Kinixys belliana*, *K. homeana*, *K. erosa*; all are represented only by a lateral view and the anterior portion of the ventral view, most are repeated in Wer-muth and Mertens, 1961); Mahé, 1965 ("Testudo" *grandidieri*, braincase figured as well as whole skull); Ruckes, 1937a (side views only of *Gopherus* sp., "Testudo" *angulata*, "T." *nigrita*, "T." *denticulata*, *Kinixys erosa*, *K.*

belliana); Siebenrock, 1897 (*Psammobates* [*Testudo*] *tentorius*, sagittal section; *P. [T.] oculifer*, ear elements*, *Testudo graeca*, quadrate and prootic); Thomson, 1932 (*Testudo graeca*, low quality figures with ambiguous sutures); Vuillemin and Rabodomihamina, 1967 (*Pyxis arachnoides*, a series of figures marred by extra sutures demarcating nonexistent nasals, postfrontals, parasphenoid and paired vomers as well as mislabeled structures, e.g., "VII" for carotid foramina; repeated in Vuillemin and Rabodomihamina, 1968); Vuillemin, 1972 (*Kinixys belliana* [*Madakinixys domergei*], side and anterior nares illustrated); Williams, 1950b (*Geochelone* [*Testudo*] *denticulata*, *Gopherus polyphemus*, *Geochelone orthopygia* [*Testudo angusticeps*], dorsal and ventral view photographs, sutures ambiguous); Williams, 1952a (*Geochelone* [*Testudo*] *monensis*, side view, no sutures); Zangerl, 1957 (*Geochelone* [*Testudo*] *denticulata*, parietal foramen*).).

GENERA AT PRESENT *INCERTAE SEDIS*: Under this heading I mention fossil taxa known from described cranial material that for one reason or another is not assignable (in my opinion) to families. I am particularly loath to erect or maintain monotypic families on the grounds of insecure relationships or unique derived characters. I have also placed meiolaniids here mostly because, as in the case of *Solnhofia*, I have no idea what their relationships are (other than being Eucryptodira) despite their relatively well-known skull morphology. As opposed to the above treatment, I am listing the references after the taxon rather than vice versa.

Apertotemporalis baharijensis Stromer, 1934: The type and only known specimen was destroyed in World War II (Dehm, personal comm.). The figures are indeterminant and I regard this taxon as a *nomen dubium*. *Chitrasephalus dumonii* Dollo, 1884: Photographs of a skull in Dollo (1884) show a skull very like that of *Chitra*. I have spent some time examining the specimen but because of its poor preservation I am unable to determine its relationships, even if it is a pleurodire or cryptodire. *Crossochelys corniger* Simpson, 1937:

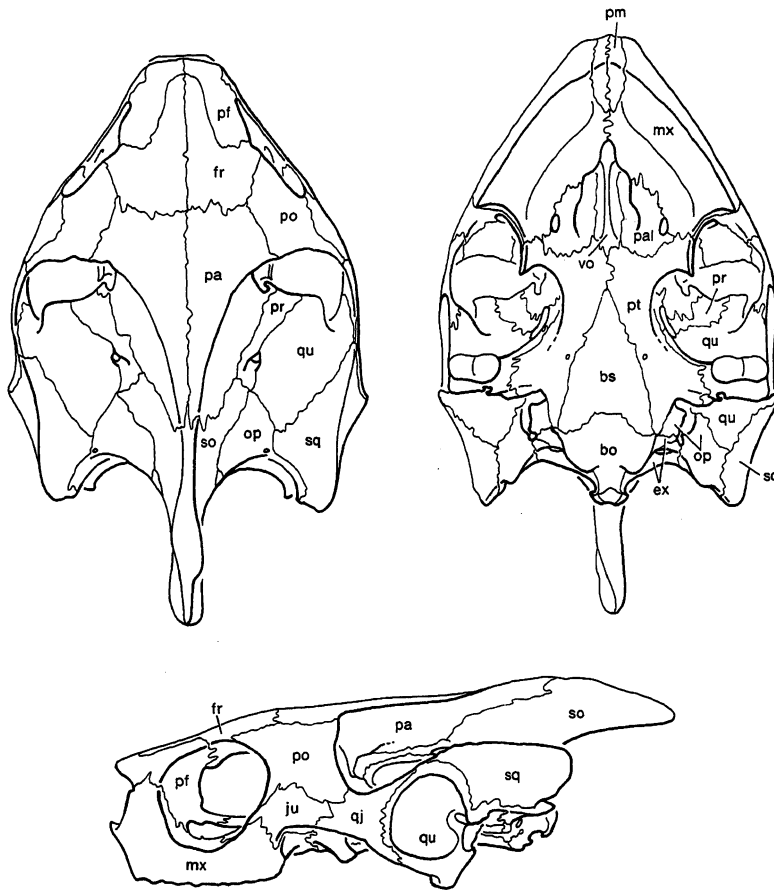


FIG. 242. *Kachuga smithii* (AMNH 85595; 37 mm.), Emydidae, near Sanghar, Sind, Pakistan.

Simpson (1938) described the disarticulated elements of this meiolaniid skull and reviewed the literature of the group. I have suggested (Gaffney, 1975d) that this group can be identified as eucryptodires. *Hangaemys hoburensis* Sukhanov and Narmandakh, 1974: This form is referred to the Macrobaenidae and the skull figured (*ibid.*, plate II) seems to have carotid foramina in the baenoid position. This region appears damaged, however, and the other skull characters are hard to determine; I do not see how it can be assigned to a family at present. *Kallokibotion bajazidi* Nopsca, 1923a: De-

scribed in Nopsca (1923b) this taxon is represented by some partial skulls and postcranial material in the British Museum (Natural History). The published figures are inaccurate with regard to sutures but enough of the skull is prepared to show the baenoid position of the foramen posterius canalis carotici interni (Gaffney, 1975d). *Macrobaena mongolica* Tatarinov, 1959: I have suggested elsewhere (Gaffney, 1972a) that the published description is inadequate to identify this as a baenoid. Dorsal and ventral views are given showing some sutures but the critical position of the foramen

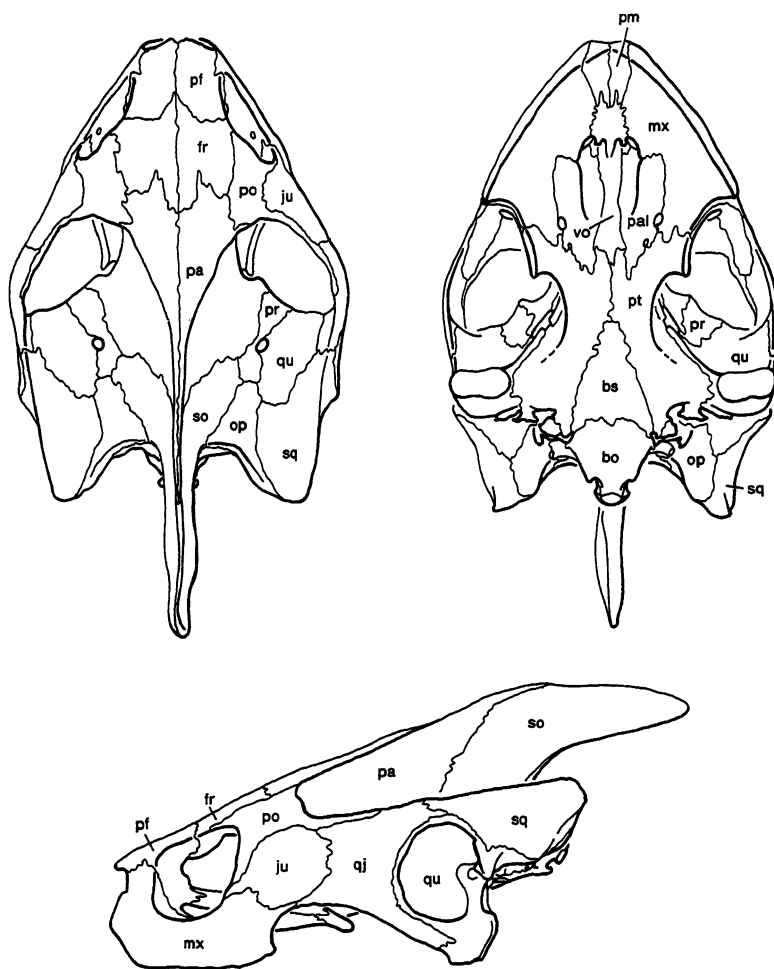


FIG. 243. *Malaclemys terrapin* (AMNH 89818; 40 mm.), Emydidae, no data.

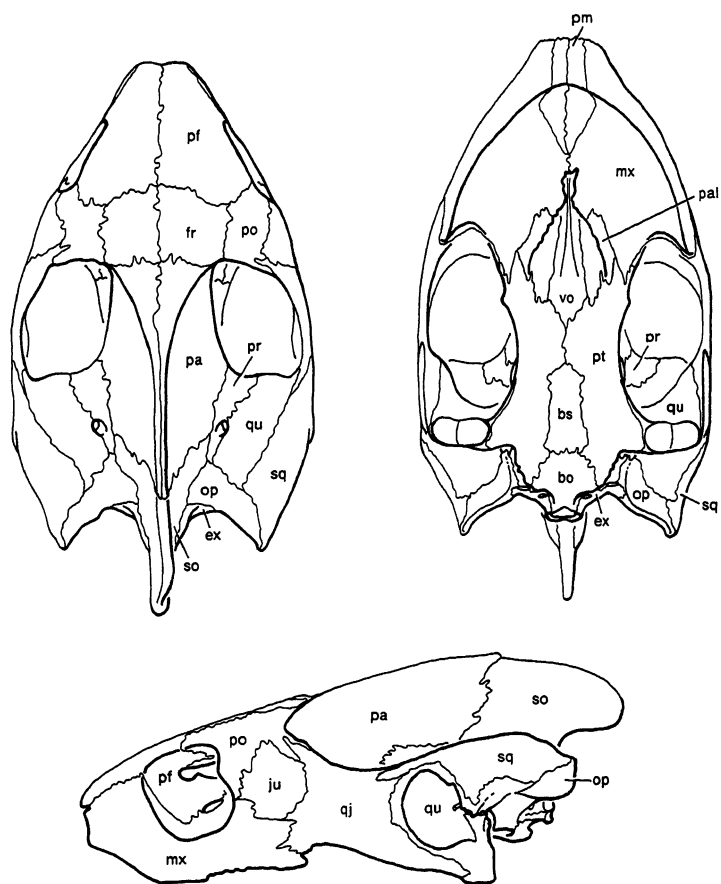


FIG. 244. *Malayemys subtrijuga* (AMNH 85978; 36 mm.), Emydidae, no data.

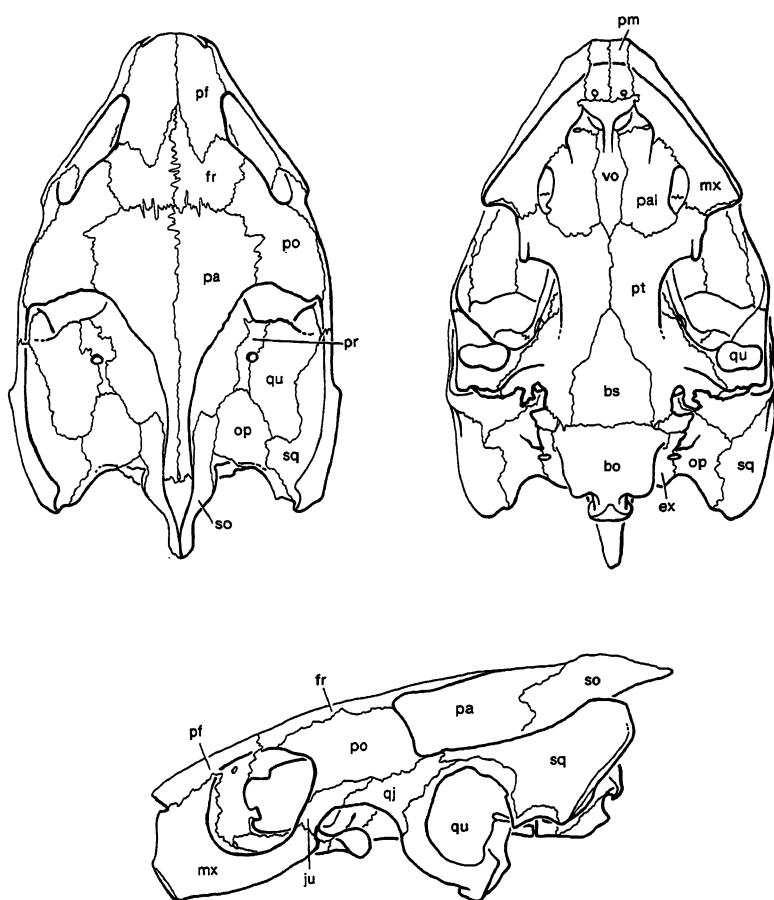


FIG. 245. *Mauremys mutica* (AMNH 84519; 38 mm.), Emydidae. Taipei, purchased in market, Taiwan, National Republic of China. *Clemmys* of Wermuth and Mertens (1961).

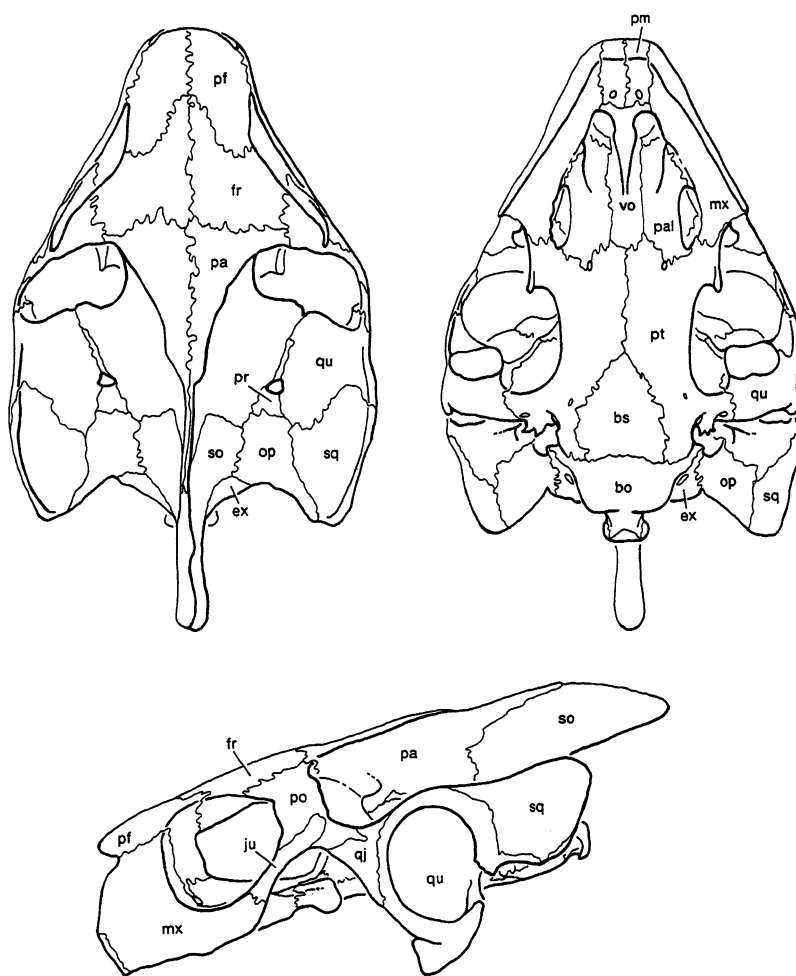


FIG. 246. *Melanochelys trijuga* (FMNH 22054; 43 mm.), Emydidae, Borneo. This species is referred to *Geoemyda* by Wermuth and Mertens (1961) and to *Nicoria* by Boulenger (1889).

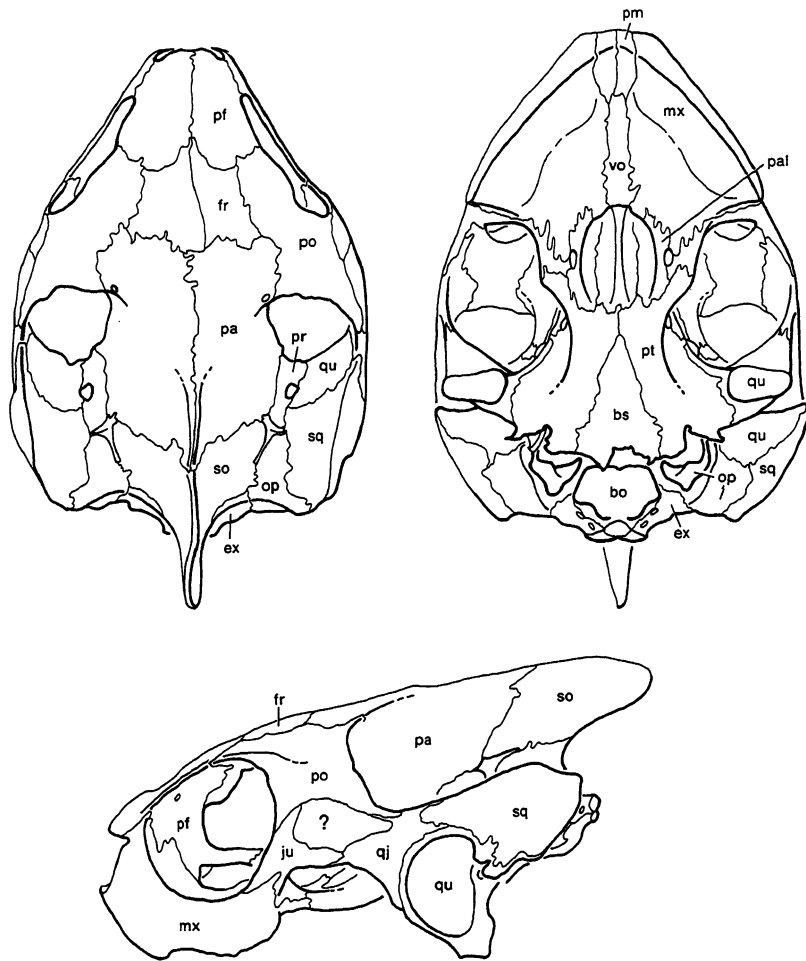


FIG. 247. *Morenia ocellata* (MCZ 3461; 22 mm.), Emydiae, Rangoon, India. The incomplete ossification of the basicranium and the prootic-opisthotic-supraoccipital suture indicates that this specimen is a juvenile. An "extra" ossification in the cheek appears to be present on both sides although it could be due to a coincidental crack within the quadratojugal of both sides.

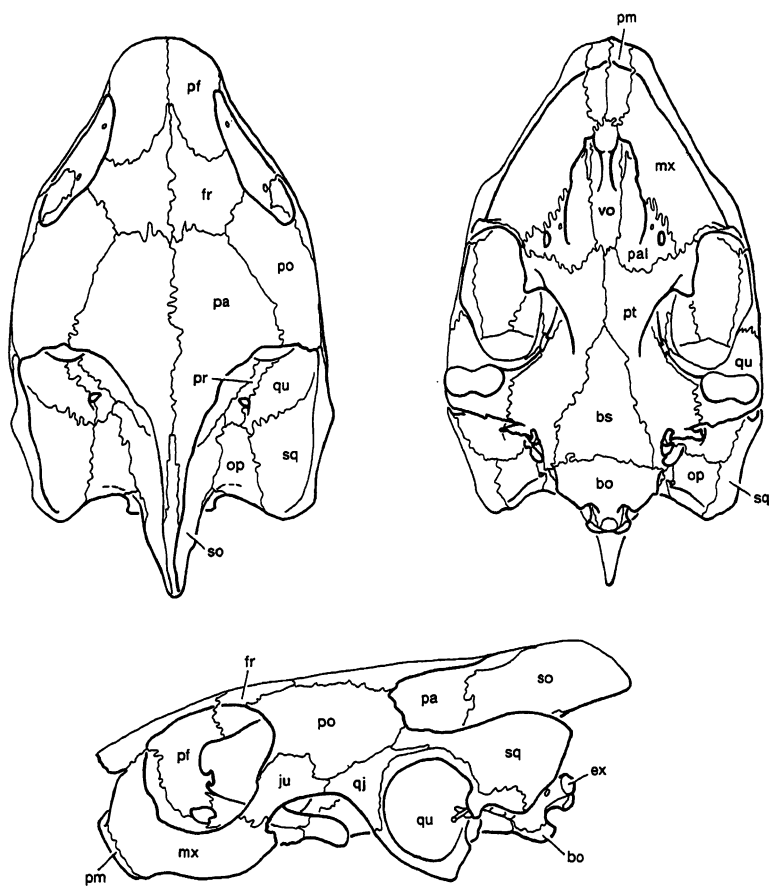


FIG. 248. *Ocadia sinensis* (AMNH 30196; 40 mm.), Emydidae, Nodola, Hainan Island, Kwangtung Province, Peoples' Republic of China.

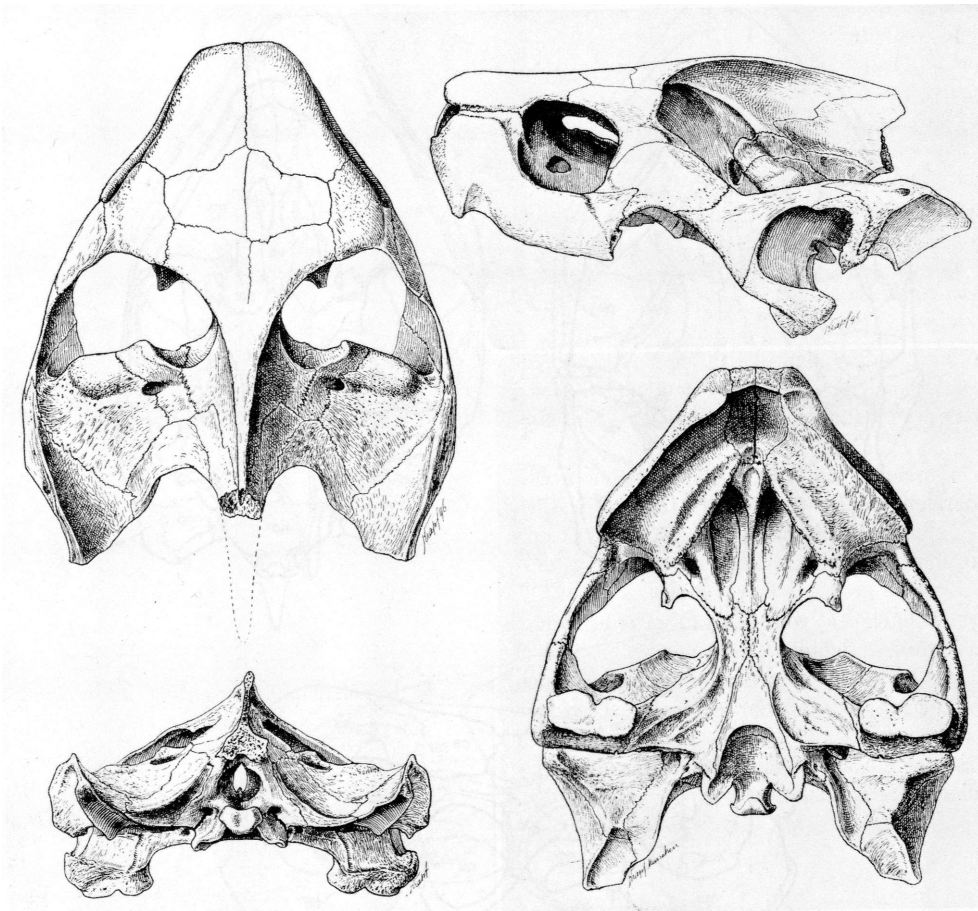


FIG. 249. *Orlitia borneensis* ("Zoology Institute of Munich"; 132 mm. *fide* Baur, 1896), Emydidae. From Baur (1896) who named this specimen as the type of a new genus and species *Adelochelys crassa*.

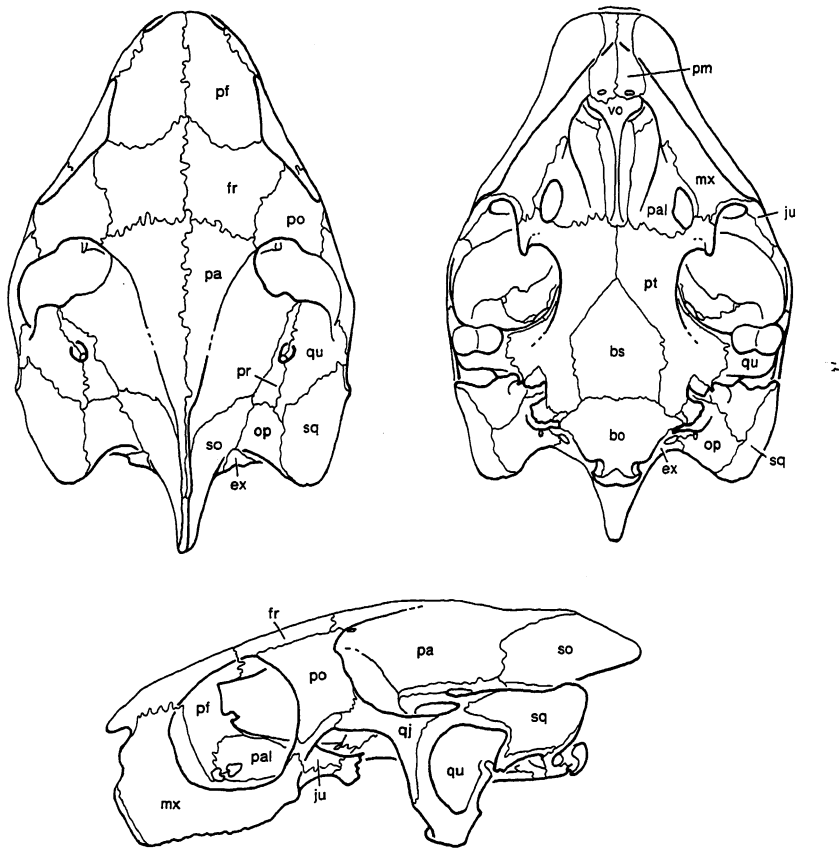


FIG. 250. *Rhinoclemys annulata* (AMNH 12430; 32 mm.), Emydidae, Sixicus Creek, near junction with Rio Grande, Nicaragua. Referred to *Geoemyda* by Wermuth and Mertens (1961) and to *Nicoria* by Boulenger (1889).

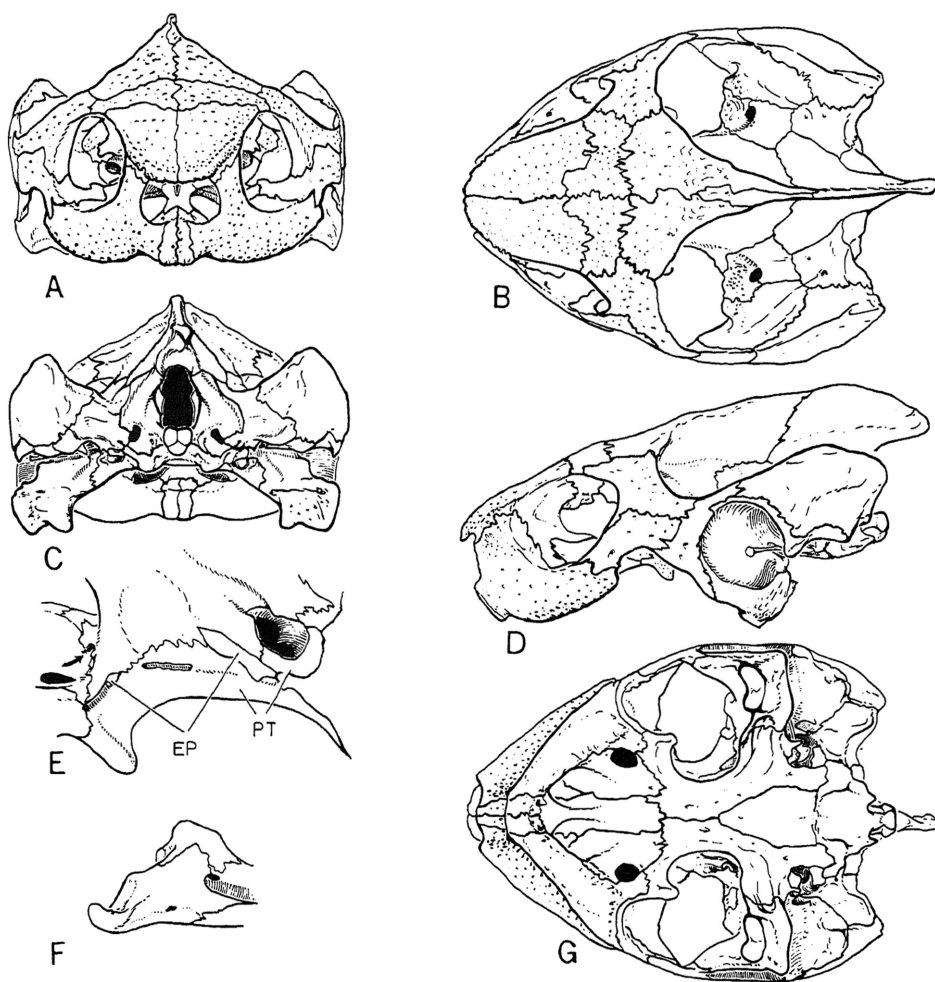


FIG. 251. *Siebenrockiella crassicollis*, Emydidae. A. Anterior. B. Dorsal. C. Occipital. D. Lateral. E. Left ethmoid region (arrow points to foramen nervi vidiani. EP, epipterygoid. PT, pterygoid). F. Medial surface of left lower jaw ramus. G. Palatal. From McDowell (1964).

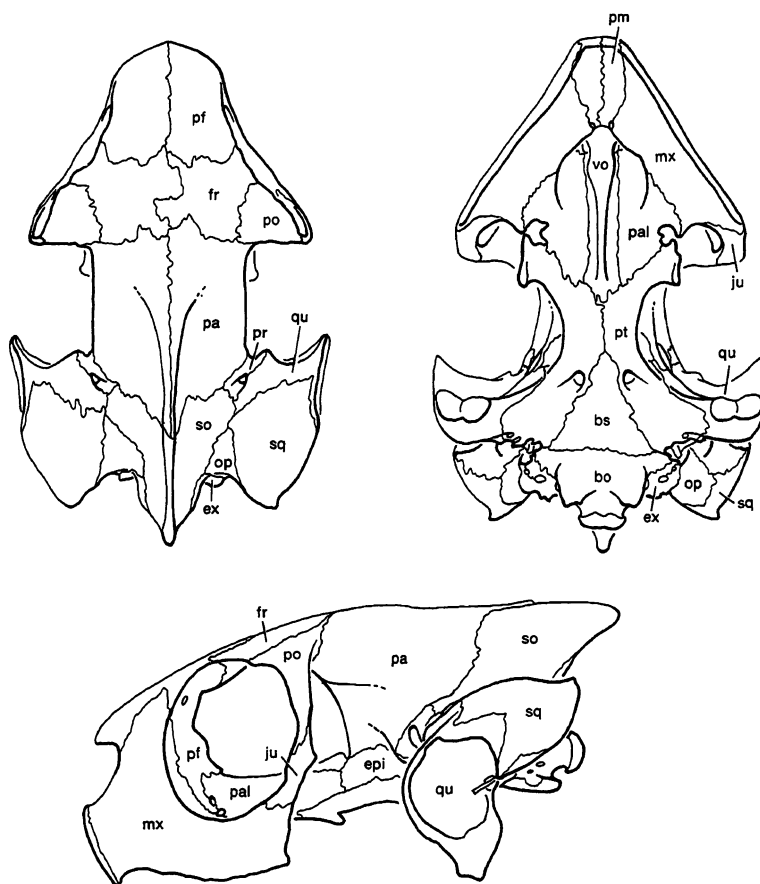


FIG. 252. *Terrapene ornata* (AMNH 71303; 32 mm.), Emydidae, Culberson County, Texas.

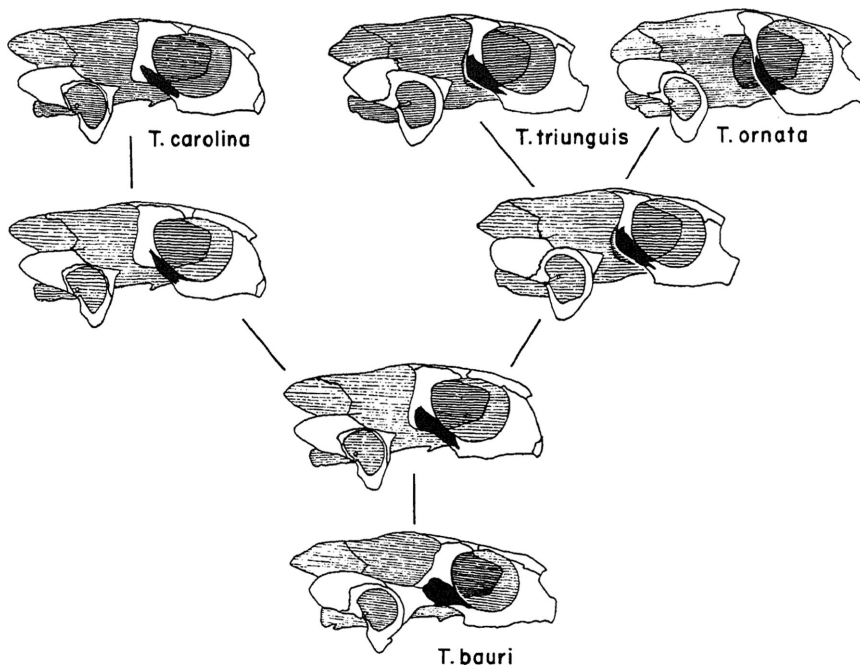


FIG. 253. Species of *Terrapene*, Emydidae, no data, as arranged by Zangerl (1948b) to suggest the steps involved in the reduction of the bony cheek and loss of the quadratojugal in *T. ornata*. The unlabeled skulls are hypothetical. From Zangerl (1948b), skulls after Taylor (1895); see also Milstead (1969) for discussion of this region.

posterius canalis carotici interni is not shown. *Meiolania platyceps* Owen, 1886: Anderson (1925) provided a good description of the skull with figures of the basicranium and ear. This paper and Simpson (1938) are excellent literature reviews for the group. I have (Gaffney, 1975d) suggested that meiolaniids are eucryptodires on the basis of the carotid foramina (see also Owen, 1880, 1888). *Nanhsiungchelys wuchingensis* Yeh, 1966: Photographs and drawings (the latter reproduced here) indicate to me the accuracy of Yeh's assignment of this form to the Cryptodira. *Niolamia argentina* (Ameghino): Woodward (1901) gave a description with some good halftones of this presumed meiolaniid (see also Simpson, 1938, for discus-

sion and further references). *Scutemys tecta* Wiman, 1930: Photographs and drawings of this small Chinese (Cretaceous) skull do not allow identification even as a cryptodire or pleurodire. *Sinemys wuerhoensis* Yeh, 1973: Photographs of this Cretaceous skull from China show the distinctive nature of this form but do not reveal useful characters except to indicate that it is a cryptodire. *Solnhofia parsonsi* Gaffney, 1975c: This form was described but not named by Parsons and Williams (1961) and further described by me (1975c). I suggest that this is a eucryptodire but was unable to determine more precise relationships. The two above cited papers make this form one of the best known fossil turtles, cranially speaking.

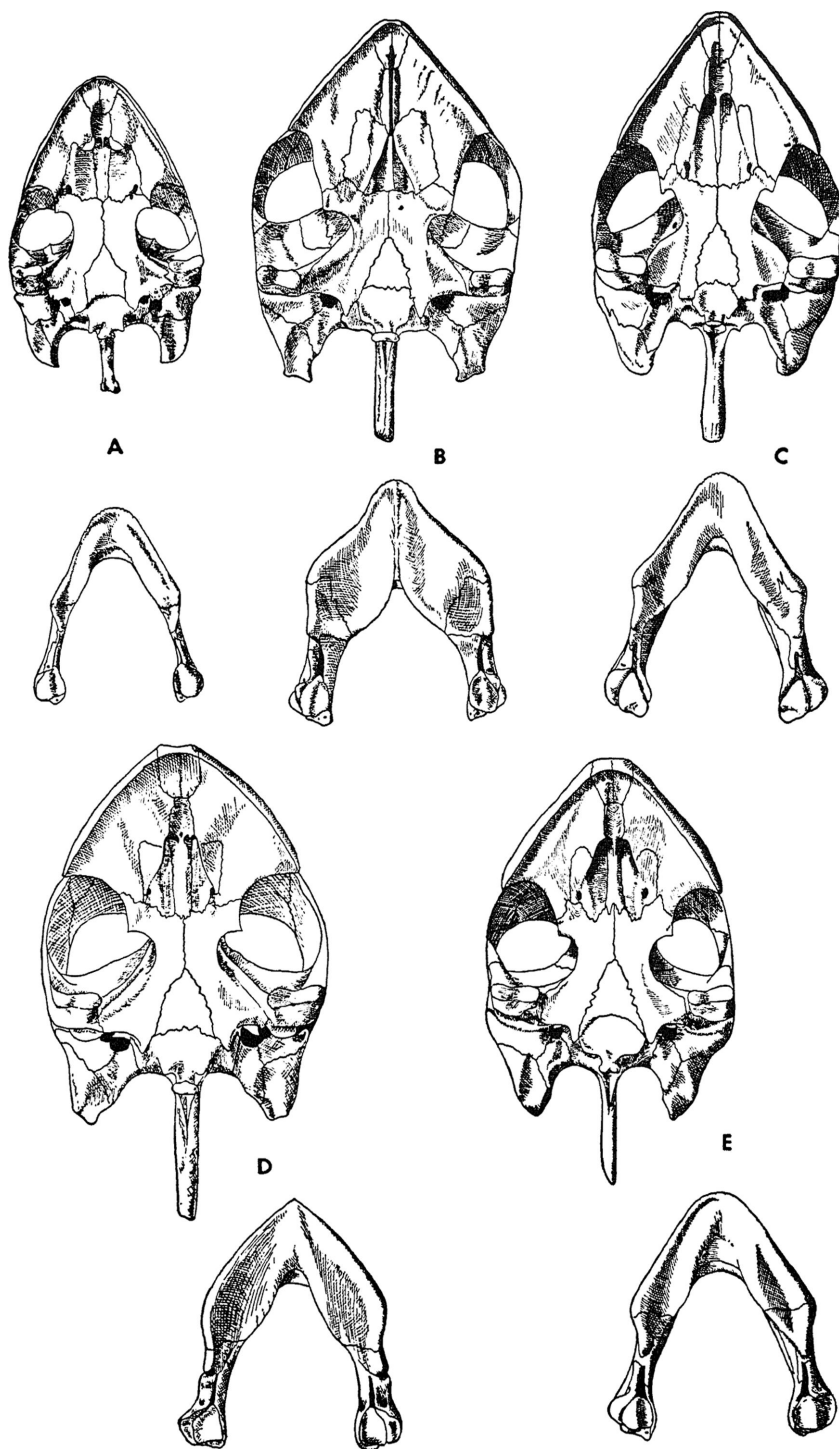


FIG. 254. Palatal views and lower jaws of *Malaclemys* and *Graptemys* (from Carr, 1952), Emydidae. A. *Graptemys pseudogeographica*. B. *Graptemys geographica*. C. *Graptemys pulchra*. D. *Malaclemys terrapin*. E. *Graptemys pseudogeographica kohnii*.

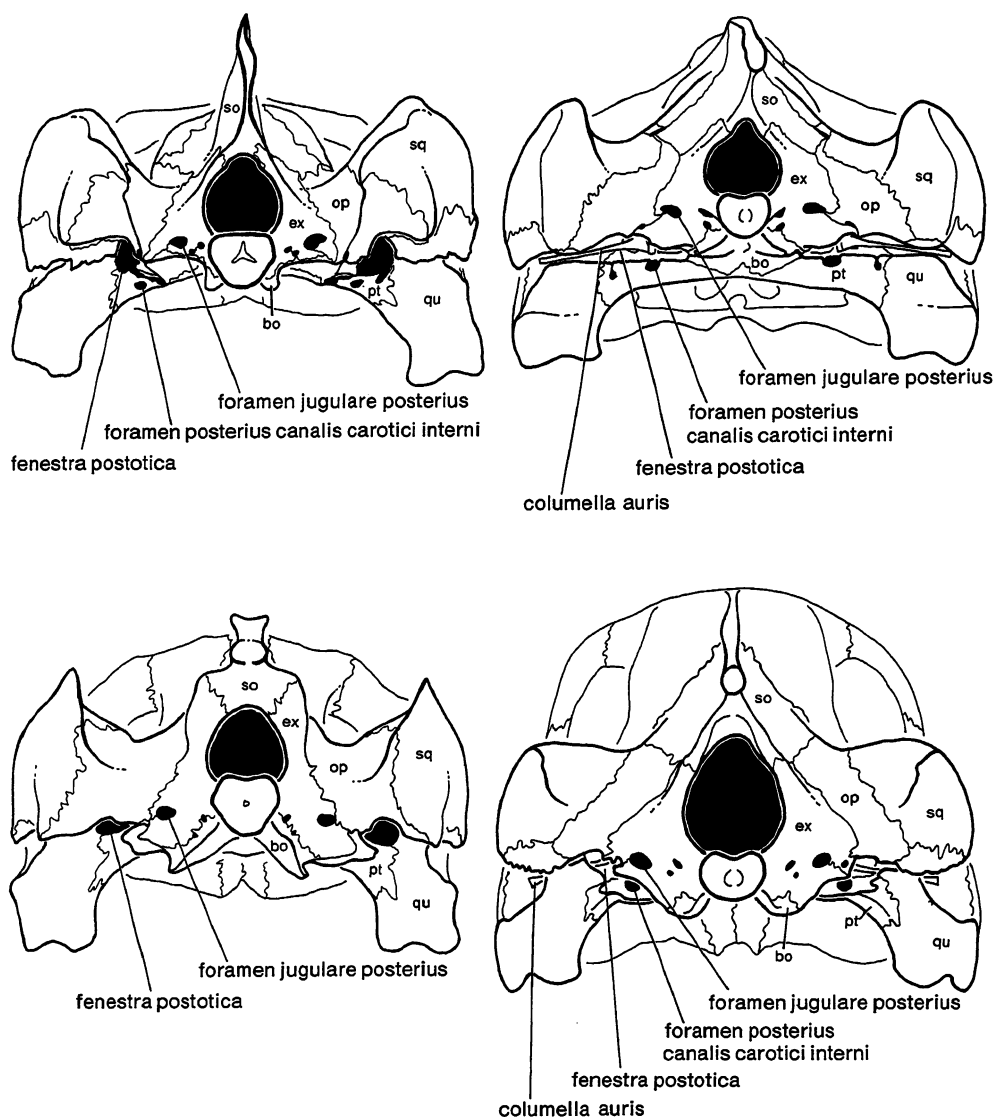


FIG. 255. Occipital views of recent Emydidae. Upper left, *Deirochelys reticularis* (AMNH 73810); upper right, *Chrysemys concinna* (AMNH 111960) referred to *Pseudemys* by Wermuth and Mertens (1961); lower left, *Mauremys mutica* (AMNH 84519) referred to *Clemmys* by Wermuth and Mertens (1961); lower right, *Terrapene ornata* (AMNH 71303).

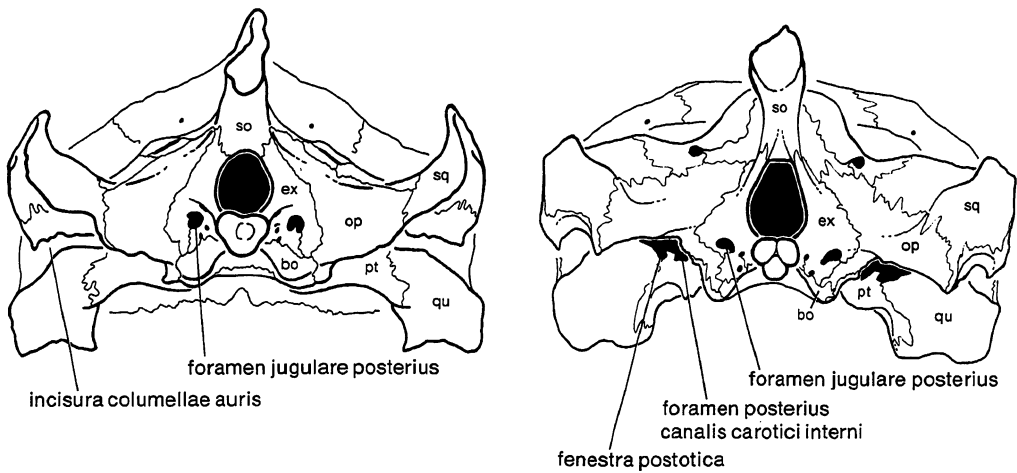


FIG. 256. Occipital views of Recent Emydidae. Left, *Batagur baska* (NMNH 29483); right, *Chinemys reevesi* (AMNH 31117).

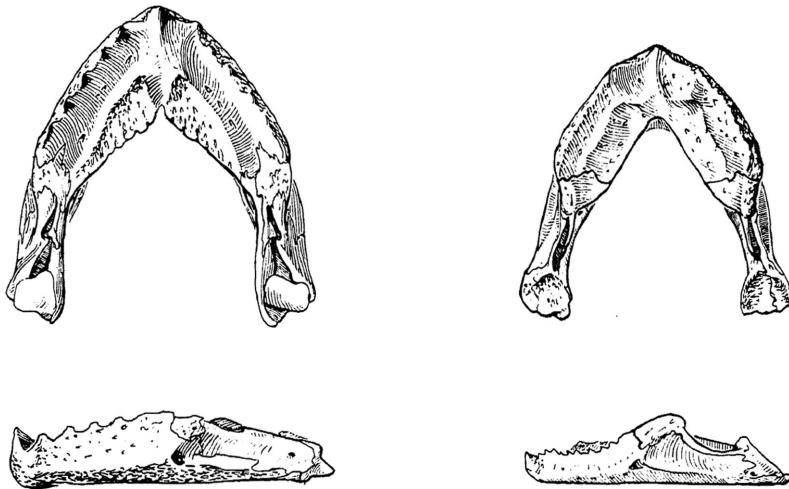
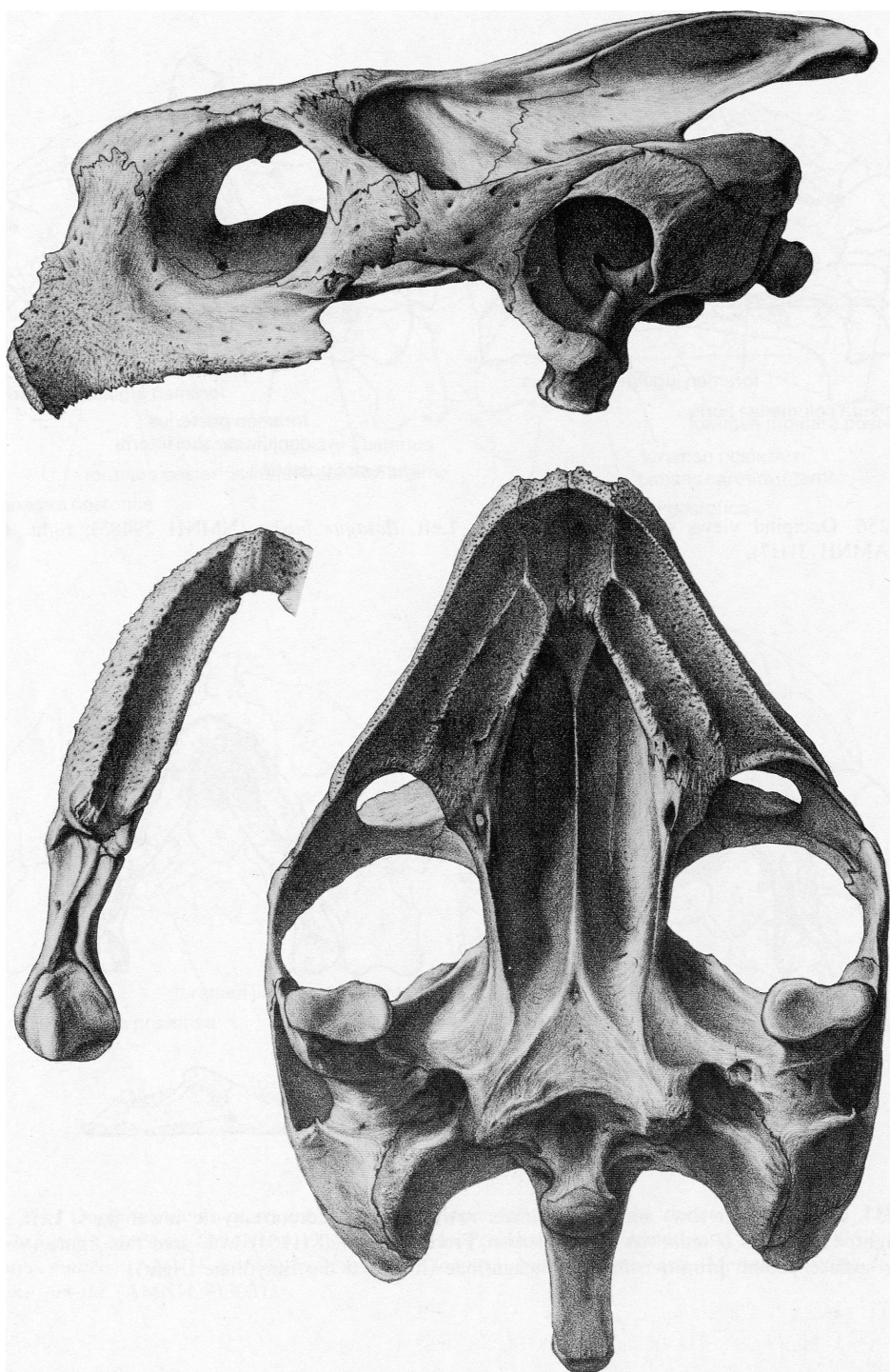


FIG. 257. Dorsal (upper row) and lateral (lower row) views of Recent emydid lower jaws. Left, *Hardella thurgii*; right, *Chrysemys (Pseudemys) alabamensis*. From McDowell (1964) who used this figure to suggest a triturating surface pattern primitive for the Batagurinae (left) and the Emydinae (right).



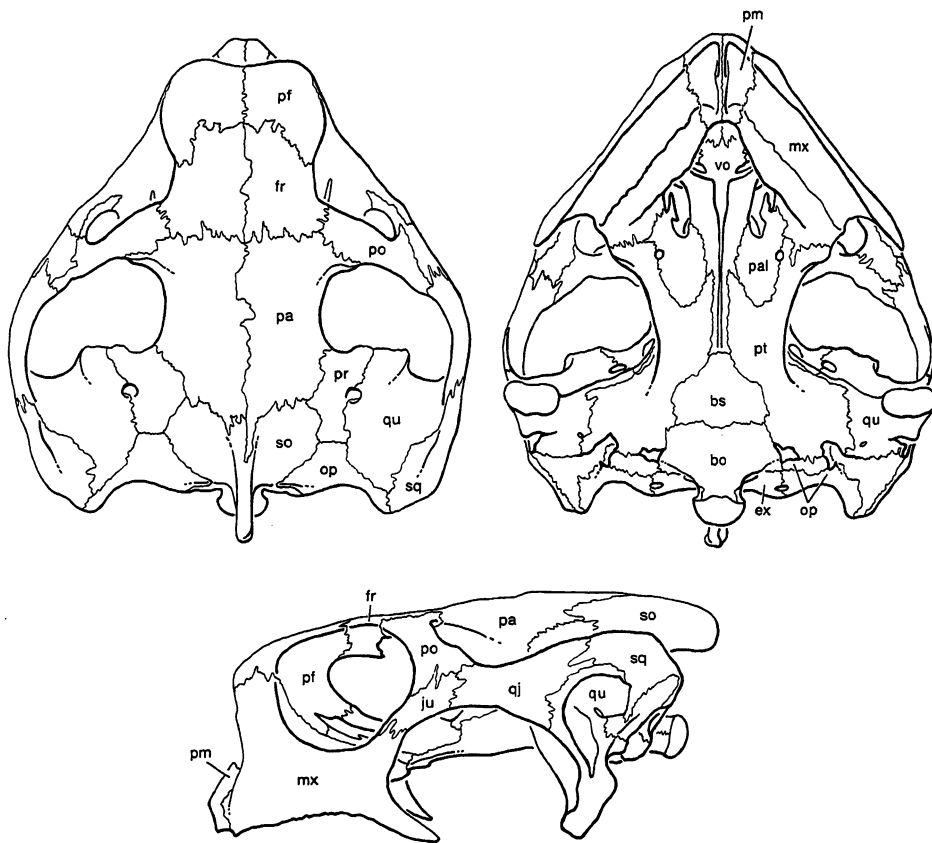


FIG. 259. *Gopherus polyphemus* (NMNH 51490; 47 mm.), Testudinidae, no data.

FIG. 258. *Geochelone (Chelonoidis) elephantopus* (BMNH, ca. 120 mm.), Testudinidae, presumably from Tagus Cove, Albemarle Island, Galapagos Islands. Modified from Günther (1877), *q.v.* for other figures. Specimen originally referred to *Testudo microphyes* (*ibid.*).

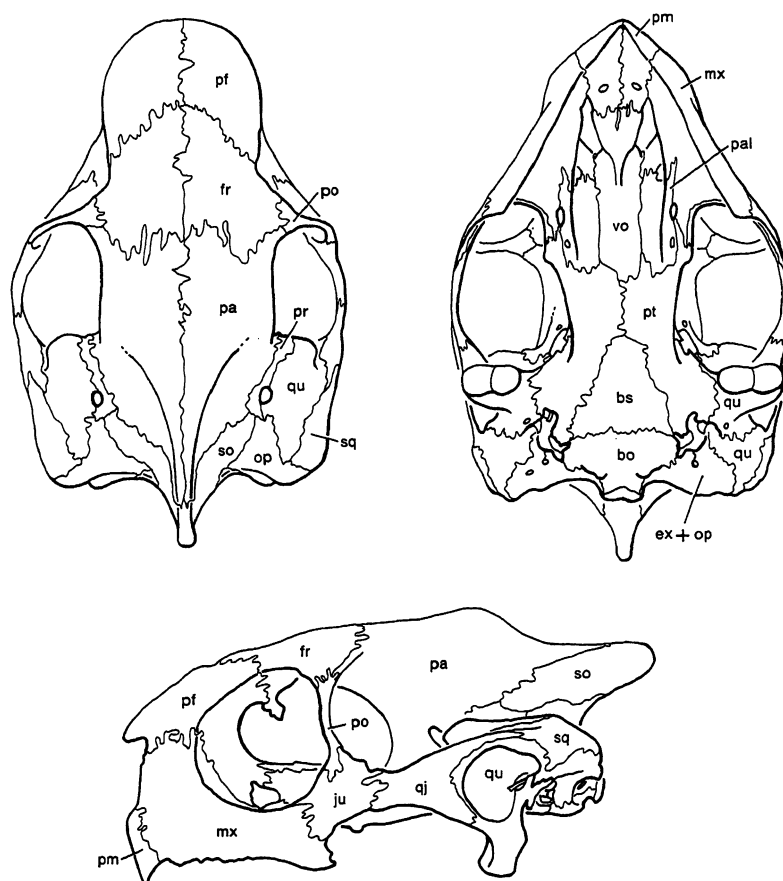


FIG. 260. *Homopus areolatus* (AMNH 17792; 21 mm.), Testudinidae, no data.

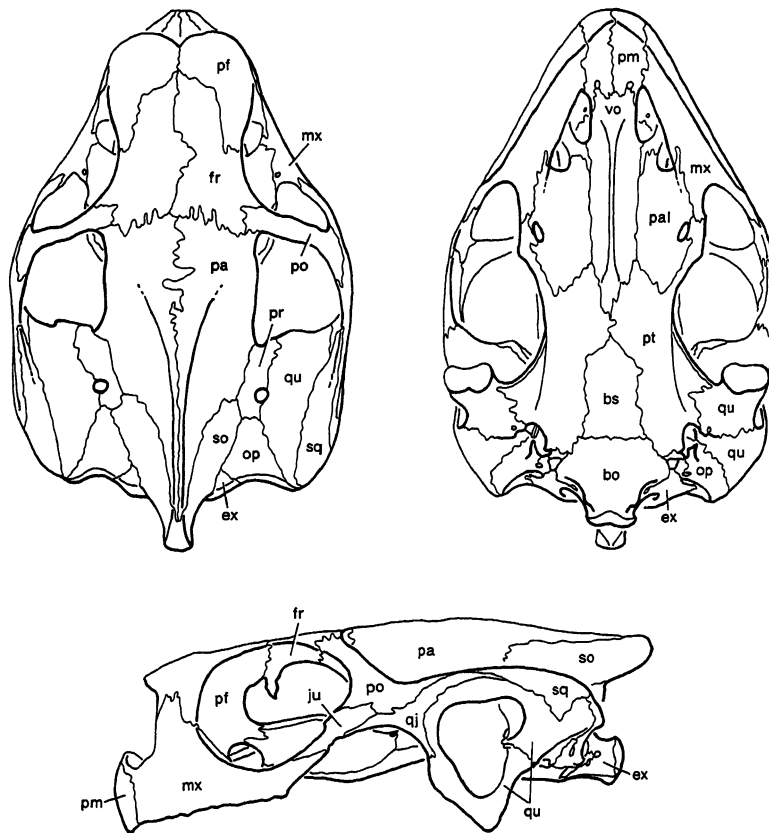


FIG. 261. *Kinixys homeana* (AMNH 43306; 40 mm.), Testudinidae, West Africa.

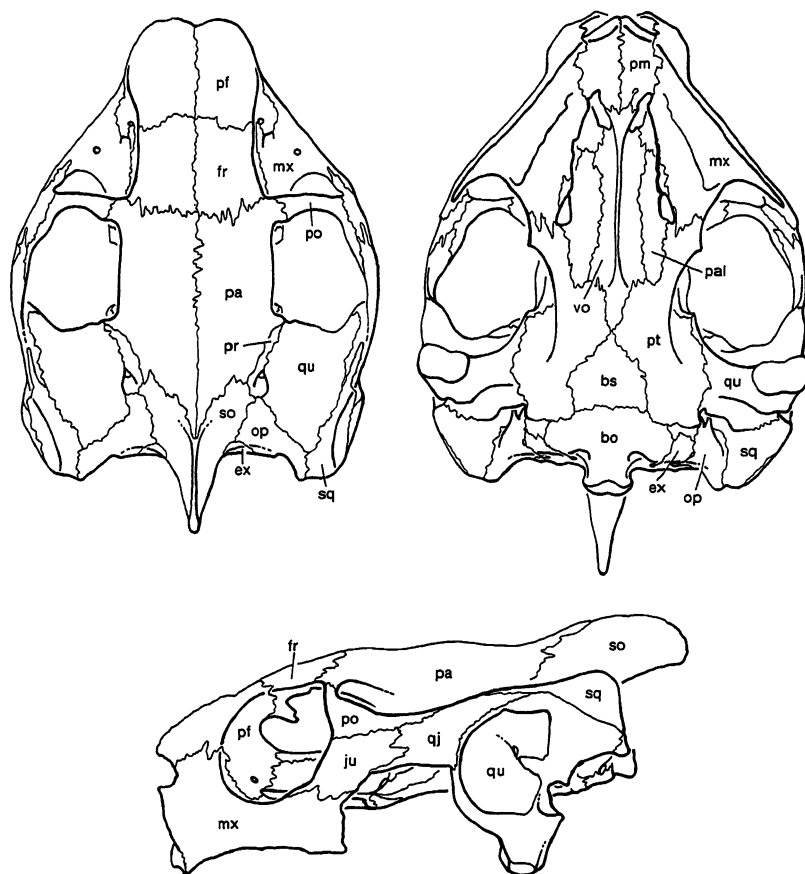


FIG. 262. *Malacochersus tornieri* (AMNH 45081; 29 mm.), Testudinidae, "Africa."

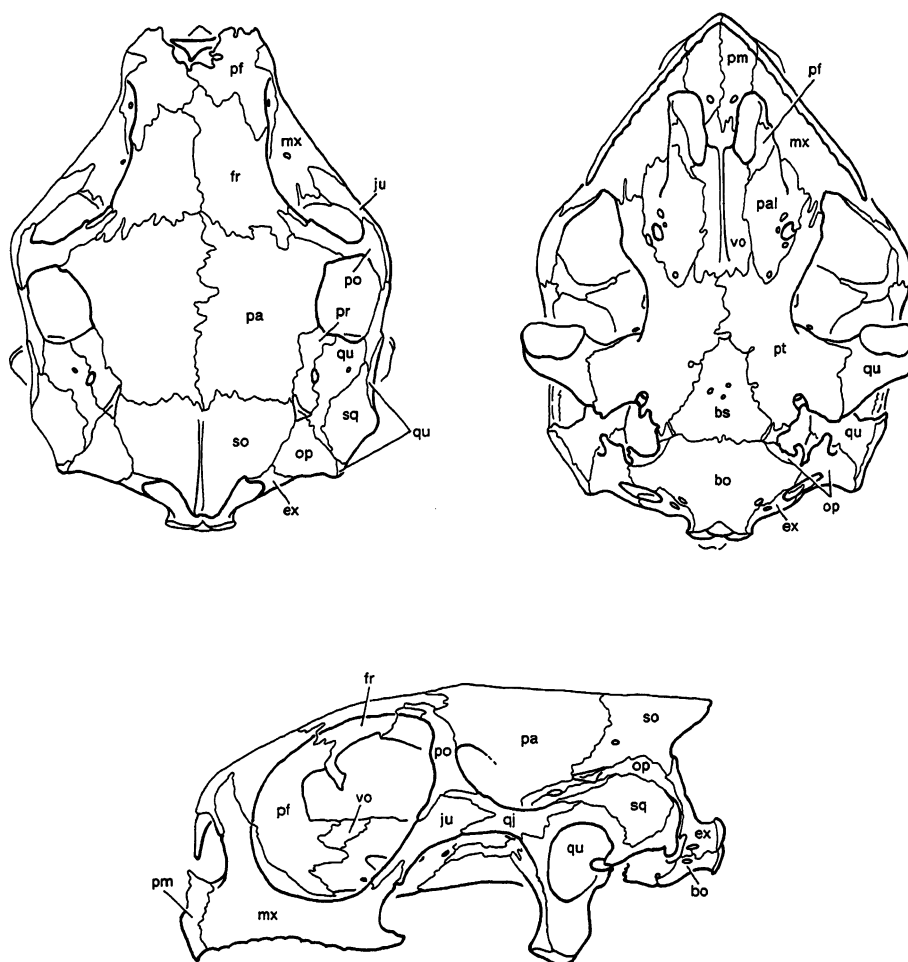


FIG. 263. *Pyxis arachnoides* (AMNH 71398; 16 mm.), Testudinidae, Amboasary, Malagasy Republic. Presumably a juvenile.

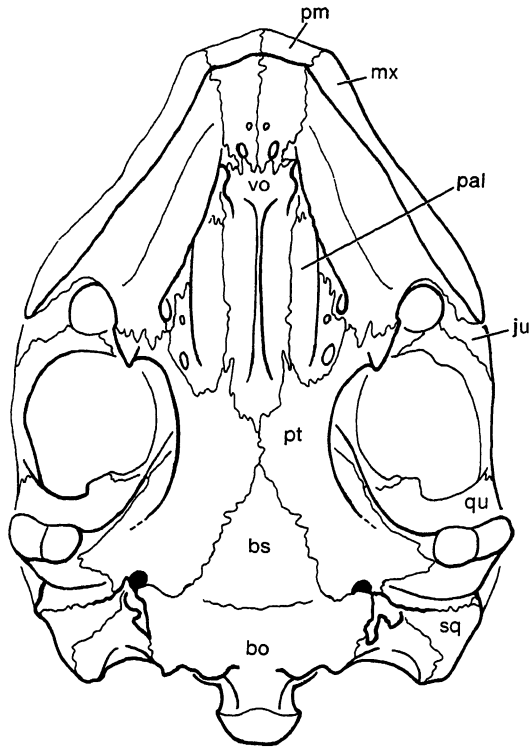


FIG. 264. *Testudo (Testudo) graeca* (AMNH 96936; 46 mm.), Testudinidae, Konya Vilati, Juberde Seydischir, Turkey. See also figures 255, 256.

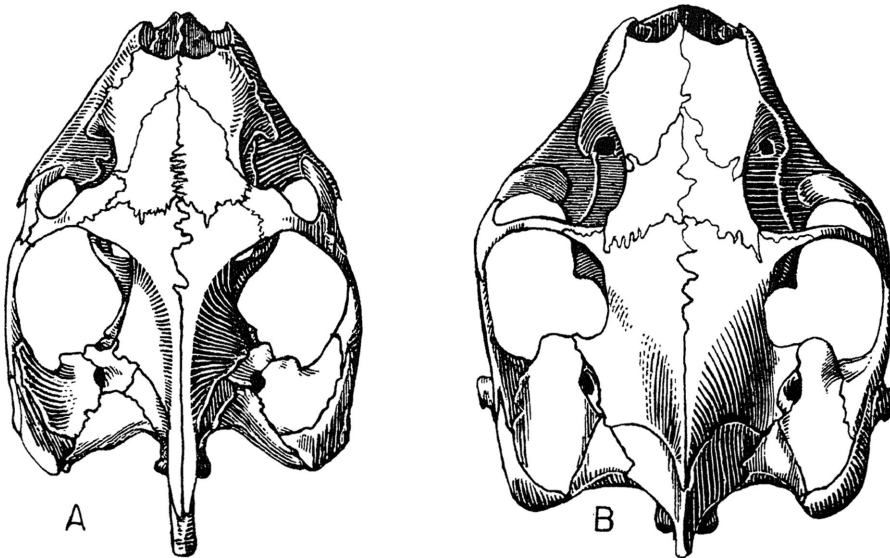


FIG. 265. Dorsal views of two Recent testudinid genera. A. *Geochelone (Geochelone) pardalis babcocki* (AMNH 7203). B. *Testudo (Testudo) graeca* (MCZ 4485). From Loveridge and Williams (1957). One of the criteria used by these authors to differentiate *Testudo* and *Geochelone* is the degree of prootic exposure seen in this figure.

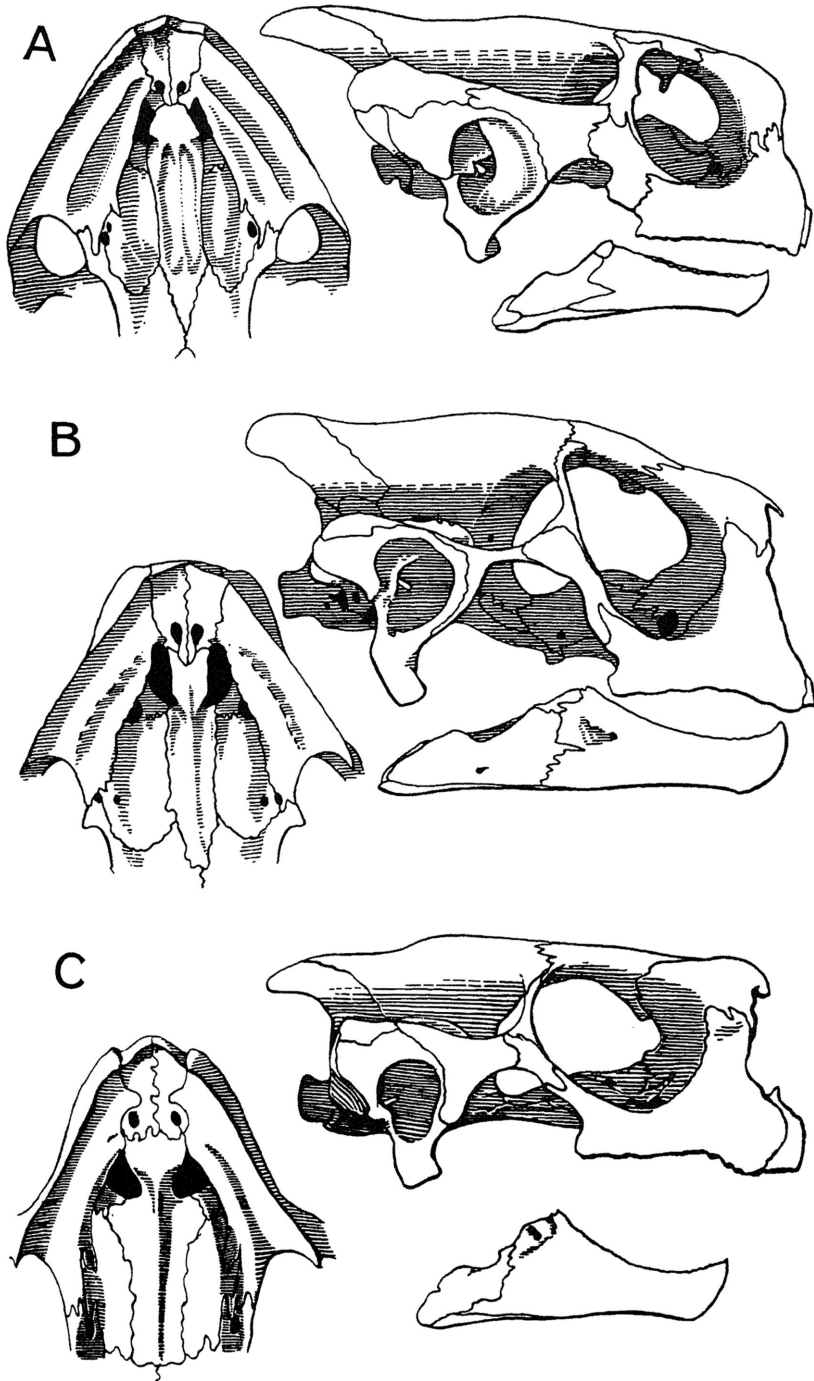


FIG. 266. Lateral and palatal views of some Recent testudinid genera. A. *Geochelone* (*Geochelone*) *pardalis babcocki* (AMNH 7703, a preoccupied number; 81 mm.). *Testudo* (*Testudo*) *graeca* (MCZ 4485; 26 mm.). C. *Psammobates oculifer* (AMNH 7094; 23 mm.). From Loveridge and Williams (1957).

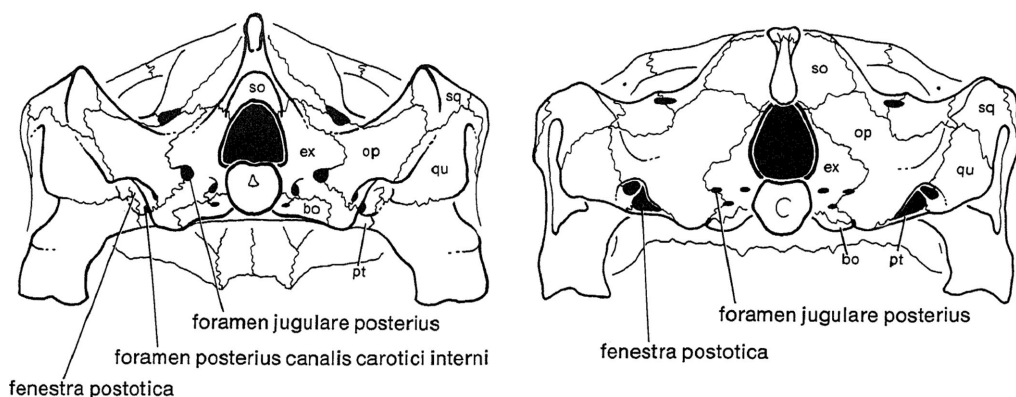


FIG. 267. Occipital views of recent Testudinidae. Left, *Malacochersus tornieri* (AMNH 45081); right, *Gopherus polyphemus* (NMNH 51490).

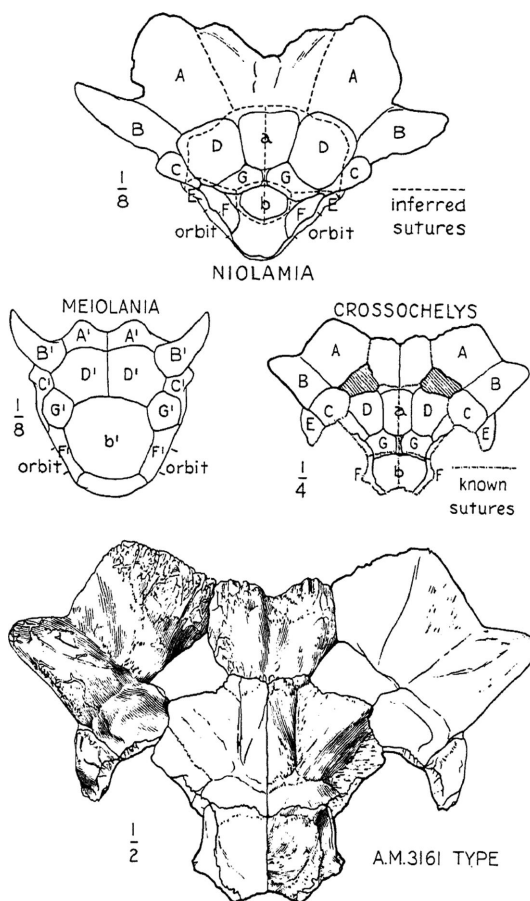


FIG. 268. Dorsal views of meiolaniid skulls. Letters indicate hypothesized homologies of scales, the comparison with *Meiolania* is particularly questionable. The lower figure is a partially restored dorsal view of the supraoccipital, left frontal, left parietal, and right squamosal in *Crossochelys corniger* (AMNH 3161). Note the temporal fenestra in *Crossochelys*, possibly a juvenile character (Simpson, 1938, p. 237). For further figures and description see Anderson (1925) and Simpson (1938). *Niolamia argentina*, pre-Oligocene, Patagonia, Argentina. *Meiolania platyceps* Pleistocene, Australia. *Crossochelys corniger*, Casamayor Formation, Eocene, southern Chubut Territory (central Patagonia), Argentina. From Simpson (1938).

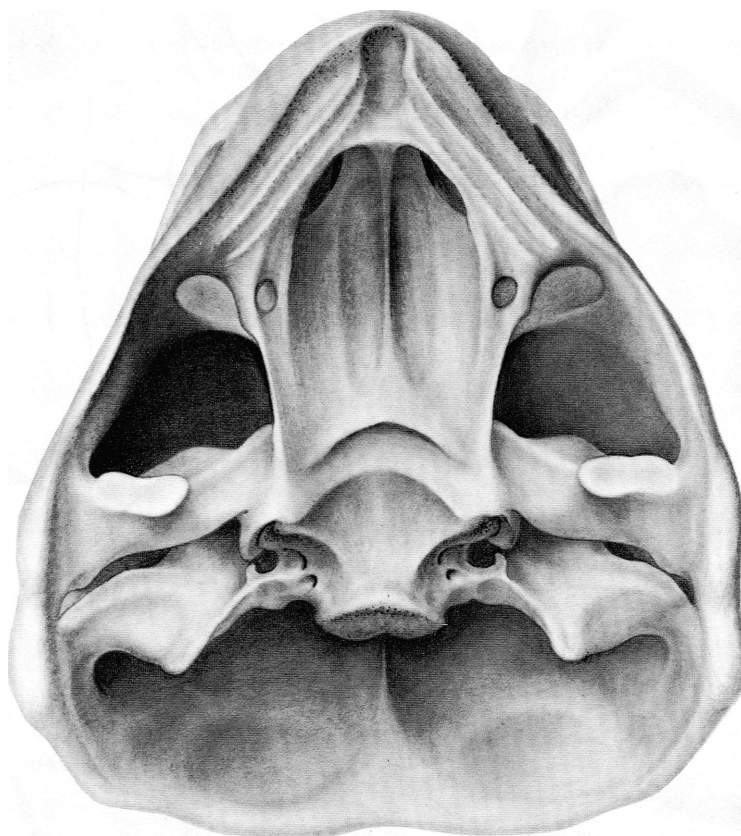


FIG. 269. *Meiolania platyceps* (Australian Museum F 43183; 134 mm.), Meiolaniidae, Pleistocene, Lord Howe Island, Australia. Palatal view with central portion of palate restored from Mining Museum F 13825a. (For further figures, description and references see Anderson, 1925).

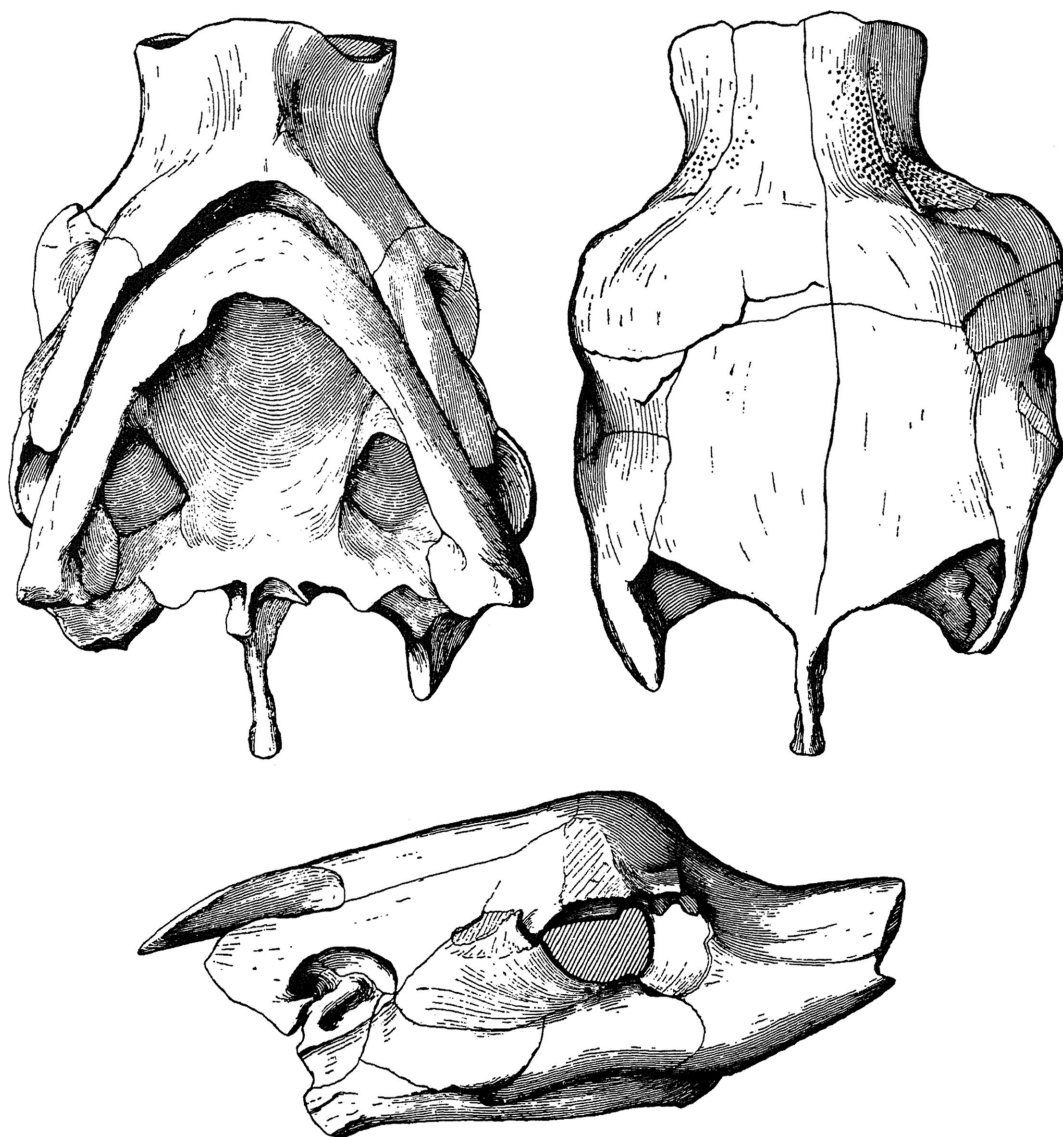


FIG. 270. *Nanhsiungchelys wuchingensis* (Inst. Vertebrate Paleontology and Paleonthropology, Peking, V. 3106; total length, including crista supraoccipital, is 285 mm.). *Cryptodira incertae sedis*, Nanhsiung Group, Late Cretaceous, Lashuhyuan, Wuching, Nanhsiung, Kwangtung, People's Republic of China. From Yeh Hsieng-K'uei (1966).

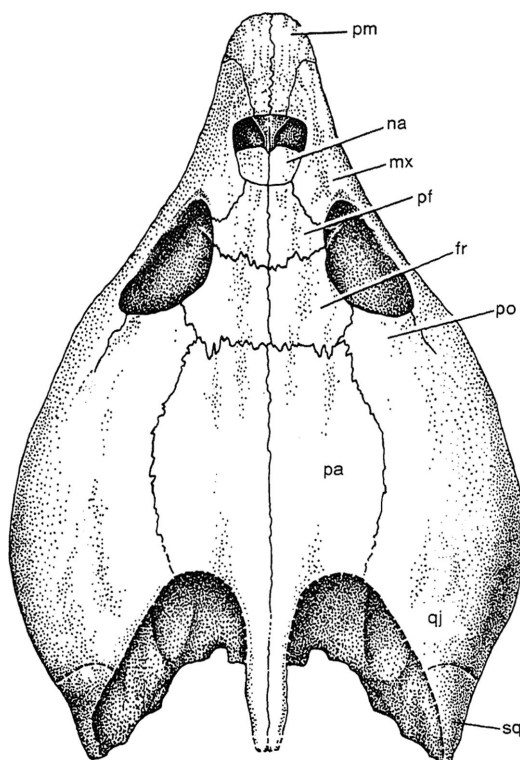


FIG. 271. *Solnhofia parsonsi* (restoration based on TM 4023, presumably Solnhofen Formation, Germany; 73 mm. as preserved, and SM 137, Solothurn, Switzerland), Eucryptodira, family *incertae sedis*, Late Jurassic. From Gaffney (1975c), *q.v.* for other figures and description; see also Parsons and Williams (1961).

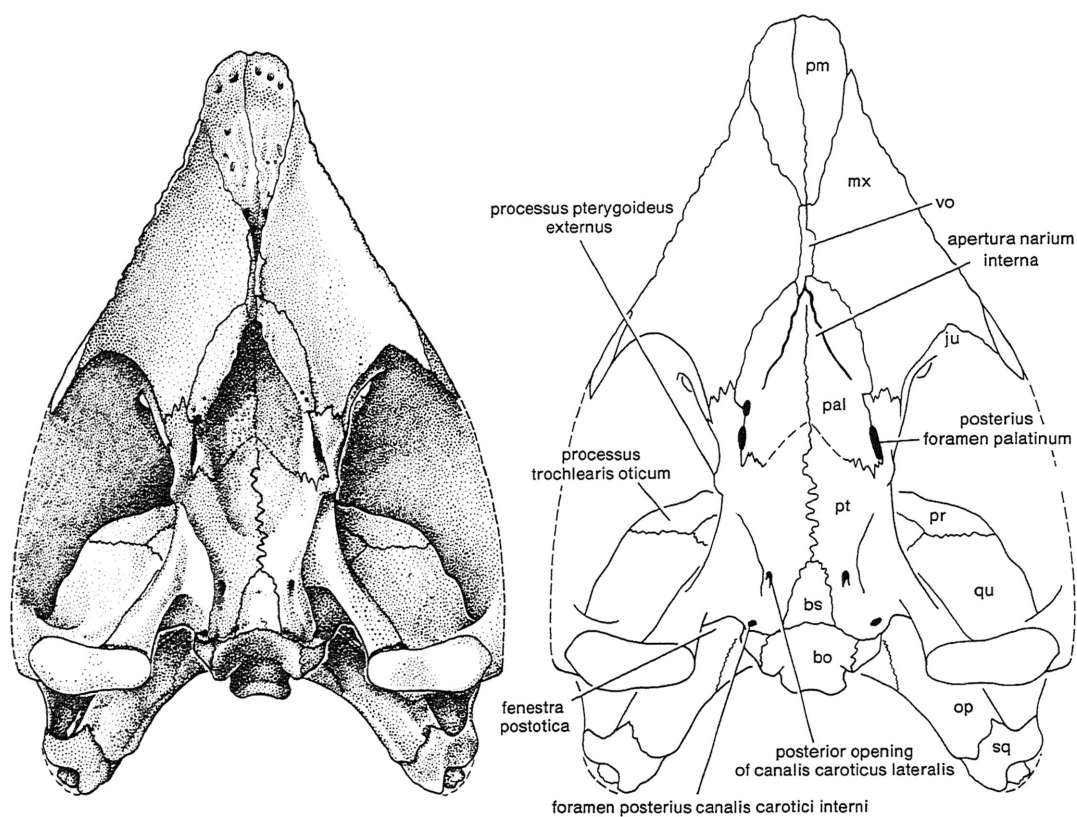


FIG. 272. *Solnhofia parsonsi* (TM 4023; 73 mm. as preserved), Eucryptodira, family *incertae sedis*, presumably Solnhofen Formation. Late Jurassic, Germany. Modified from Parsons and Williams (1961), *q.v.* for other figures and description; see also Gaffney (1975c).

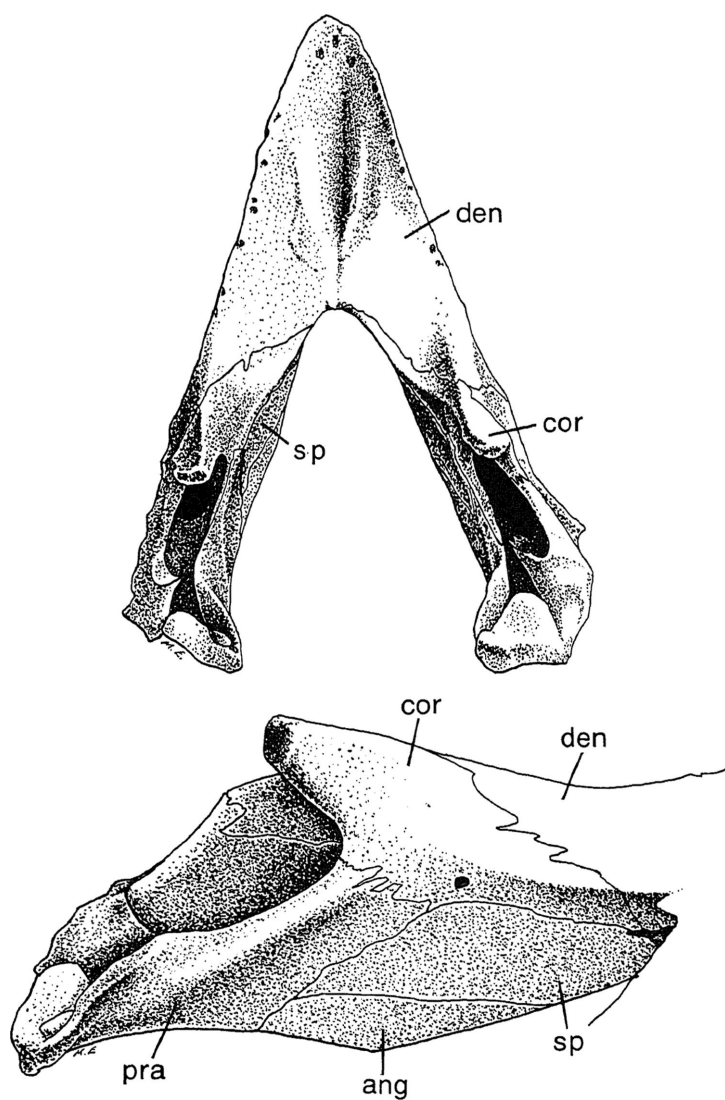


FIG. 273. *Solnhofia parsonsi* (TM 4023; 73 mm. as preserved), Eucryptodira, family *incertae sedis*, presumably Solnhofen Formation, Late Jurassic, Germany. Upper, dorsal view of lower jaw; lower, medial view of left ramus. Modified from Parsons and Williams (1961; q.v.), also see Gaffney (1975c) for other figures and description.

GLOSSARY

Although the following glossary is slightly modified (primarily by the addition of new terms and the correction of old errors) from that published in Gaffney, 1972b, I include it here with the intent of increasing the usefulness of this paper. Unfamiliar terms can be found quickly by using the glossary while reading the text. The glossary also contains references for the main text discussions and a few of the most useful figure references for each term. Parsons and Williams (1961) should be consulted for synonyms of these terms and Gaffney (*ibid.*) for figure references in the literature (not repeated here).

ADITUS CANALIS STAPEDIO-TEMPORALIS—The posteroventral opening of the *canalis stapedio-temporalis* into the roof of the *cavum acustico-jugulare*; in most cases formed by the quadrate and prootic. The *arteria stapedia* passes through it. See *cavum acustico-jugulare*, figs. 10, 30-32.

ANTRUM POSTOTICUM—Generally a cone-shaped cavity with apex pointing posteriorly and base opening anteriorly into the posterodorsal region of the *cavum tympani* into which it grades gradually in most genera. The *incisura columellae auris* in most cases marks the anteroventral limits of the *antrum*. The *antrum* is formed by the squamosal and quadrate. See squamosal, figs. 53, 63, 65, 132.

APERTURA NARIUM EXTERNA—The external bony openings of the nares; formed by the prefrontals, maxillae, premaxillae and, in some groups, nasals, see fig. 2.

APERTURA NARIUM INTERNA—The internal bony opening of the nares, in most cases on the palate. The bones involved vary somewhat. In most turtles (*Chelydra*, for example) the vomer, maxilla, and palatine bones outline the *apertura*. In most pelomedusids the vomer is lost, whereas in many chelonoids (particularly living chelonids) the development of a secondary palate excludes the maxillae; the palatines and vomer are the principal elements. See maxilla, figs. 9, 18, 19.

AREA ARTICULARIS MANDIBULARIS—The area on the lower jaw that articulates with the *condylus mandibularis* of the quadrate; consists primarily of the articular bone. See articular, figs. 111, 112.

BASIS COLUMELLAE—The medial, expanded end of

the *columella auris*, fits into the *fenestra ovalis*. See *columella auris*.

BASIS TUBERCULI BASALIS—An oval tubercle generally situated on the midline of the skull at the union of the basisphenoid and basioccipital. Most of the tubercle is generally on the latter bone. "Gives attachment to the bifid ligament of the medulla" (Kesteven, 1910, p. 376). See basioccipital, figs. 60, 65.

CANALIS ALVEOLARIS INFERIOR—A canal extending anteriorly for most of the length of the dentary, beginning at the *foramen alveolare inferius*. Soliman (1964, figs. 11-13) indicated that the *ramus alveolaris inferior* (V_4), the *ramus cutaneus externus* (V_3), and small blood vessels traverse the *canalis*. See dentary, fig. 104.

CANALIS ALVEOLARIS SUPERIOR—This canal roughly parallels the lateral edge of the outer maxillary surface on the floor of the *fossa orbitalis*; has connections to the *foramen alveolare superius* and the *canalis infraorbitalis*. "The superior alveolar artery goes through the foramen alveolare superius and into the *canalis alveolaris superior*" (Albrecht, 1967, p. 90). See maxilla, figs. 30-33.

CANALIS CAROTICO-PHARYNGEALIS—A canal formed in the pterygoid bone, directed and opening ventrally, and communicating dorsally with the *canalis caroticus lateralis*. Albrecht (1967, pp. 85, 86) reported it in *Chrysemys* and *Sternotherus*. The *arteria carotico-pharyngealis* is transmitted by this canal. See pterygoid.

CANALIS CAROTICUS INTERNUS—A pair of canals curving anteromedially, from the posterior region of the skull through the basicranium to an opening in the basisphenoid at the posterior end of the *sella turcica*; in most cases formed at least in part by the pterygoid, basisphenoid and sometimes the prootic; contains the *arteria carotica interna*. See pterygoid and prootic, figs. 30-34.

CANALIS CAROTICUS LATERALIS—"In *Chrysemys*, *Sternotherus*, and *Trionyx*, the *canalis caroticus* on each side of the skull gives off an anterior canal in the pterygoid bone which opens into the sulcus cavernosus directly lateral to the basisphenoid" (Albrecht, 1967, p. 84). The "anterior canal" is the *canalis caroticus lateralis* and carries the *arteria palatina* in the first two genera and the *arteria pseudopalatina* in *Trionyx*. See pterygoid, figs. 30, 31, 33.

CANALIS CARTILAGINIS MECKELII—Any part of the

sulcus cartilaginis meckelii that is roofed over by bone to form a canal. See dentary.

CANALIS CAVERNOSUS—The canal that is continuous posteriorly with the *sulcus cavernosus* (and is essentially the *sulcus* closed over); runs on the floor of the *cavum cranii* on either side of the basisphenoid posterolaterally beneath the *aditus canalis stapedio-temporalis* and into the *cavum acustico-jugulare*. The *canalis* and *sulcus* contain the *vena capitis lateralis* and represent the cranioquadrate space of other vertebrates. See pterygoid and *cavum acustico-jugulare*, fig. 10.

CANALIS CHORDA TYMPANI MANDIBULARIS—The canal in the lower jaw that contains the chorda tympani branch of the facial (VII) nerve; formed in most cases by the articular and prearticular bones. See prearticular, fig. 104.

CANALIS CHORDA TYMPANI QUADRATI—The canal in the quadrate bone between the *foramen chorda tympani superius* and the *foramen chorda tympani inferius*. The chorda tympani branch of the facial (VII) nerve exits from the skull via this canal. See quadrate, fig. 10.

CANALIS INFRAORBITALIS—A canal beginning medially at the *foramen supramaxillare* and extending anterolaterally to the *canalis alveolaris superior*; contains the *arteria supramaxillaris* in *Chrysemys*, *Sternotherus*, and *Trionyx* (Albrecht, 1967); is in most cases contained in the maxilla. See maxilla, figs. 30-33.

CANALIS INTRAPALATINUS—A canal found in *Trionyx* (but not in *Sternotherus* or *Chrysemys*) that connects the *foramen palatinum accessorium* with the *foramen palatinum posterius* and is formed by the palatine bone (Albrecht, 1967, p. 88); transmits a small branch of the *arteria inframaxillaris*.

CANALIS NERVI ABDUCENTIS—A paired canal in the lateral part of the *dorsum sellae* in the basisphenoid. The abducent (VI) nerve traverses this canal. See basisphenoid, fig. 44.

CANALIS NERVI VIDIANI—A canal that extends anteriorly along the side of the basicranium in the pterygoid and/or palatine bones; in most cases begins in the *foramen pro ramo nervi vidiani* and ends in the *foramen palatinum posterius* in cryptodires. The palatine branch (vidian nerve) of the facial (VII) nerve and in some cases, small arteries (Albrecht, 1967) traverse the *canalis*. Albrecht (*ibid.*) differentiated between an anterior and posterior part of the *canalis*. He (*ibid.*, p. 87) described the nerves and arteries in this area. See pterygoid, figs. 21, 28, 30, 31, 33.

CANALIS SEMICIRCULARIS ANTERIOR—Strictly speaking the term *canalis semicircularis* should refer only to the membranous endolymphatic canals of

the inner ear and not to the bony canals which contain them. The bony canals are variable in their enclosure of the membranous canals which tend to be rather consistent in vertebrates. However, it is common practice to use the term *canalis* as I do here for the bony canals; *canalis semicircularis anterior* extends from the *recessus labyrinthicus supraoccipitalis* to the *recessus labyrinthicus prooticus*; formed by the supraoccipital and prootic. See *cavum labyrinthicum*, fig. 52.

CANALIS SEMICIRCULARIS HORIZONTALIS—Extends from the *recessus labyrinthicus prooticus* to the *recessus labyrinthicus opisthoticus*; is in most cases formed by the prootic and opisthotic. See *cavum labyrinthicum*, figs. 49, 52.

CANALIS SEMICIRCULARIS POSTERIOR—Extends from the *recessus labyrinthicus supraoccipitalis* to the *recessus labyrinthicus opisthoticus*; formed by the supraoccipital and opisthotic. See *cavum labyrinthicum*, figs. 49, 52.

CANALIS STAPEDIO-TEMPORALIS—The passage of the *arteria stapedia* from the *aditus canalis stapedio-temporalis* in the *cavum acustico-jugulare* to the *fossa temporalis superior*; formed between the quadrate and prootic. See *cavum acustico-jugulare*, figs. 10, 30-32.

CARTILAGO TRANSILIENS—The sliding sesamoid cartilage at the site of contact between the external tendon (the main adductor aponeurosis or "Bodenaponeurosis") on either the *processus trochlearis oticus* (cryptodires) or the *processus trochlearis pterygoidei* (pleurodires). This cartilage may ossify (Ray, 1959); is generally meniscus-shaped, see figs. 14, 15.

CAVUM ACUSTICO-JUGULARE—A large cavity in the posteroventral region of the skull approximately between the *cavum tympani* and the *cavum labyrinthicum*; contains the *columella auris*, the *arteria stapedia*, the *vena capitis lateralis*, the glossopharyngeal (IX) nerve, the hyomandibular (posterior) branch of the facial (VII) nerve, and the *vena cerebialis posterior*. The *processus interfenestralis* tends to separate a small area including the *recessus scalae tympani*, which is posteromedial to the main part of the *cavum*. The posterior wall of the *cavum acustico-jugulare* is in most cases unossified and named the *fenestra postotica*. The *cavum acustico-jugulare* is generally bound anteriorly and laterally by the quadrate, medially by the prootic and opisthotic, ventrally by the pterygoid, and dorsally by the quadrate and opisthotic. See *cavum acustico-jugulare*, figs. 50, 51, 64, 87.

CAVUM CRANII—The large central space occupying the area from the *fossa nasalis* to the *foramen*

magnum; is defined by bone, and an endocranial cast would be a replica of it. The brain and dura mater are the principal occupants of the *cavum* in life. Most of the median bones in the skull participate in the formation of the *cavum cranii*, figs. 66-83.

CAVUM LABYRINTHICUM—The bony inner ear cavity, formed by the prootic anteriorly, the opisthotic posteriorly, and the supraoccipital dorsally. In life, the bony capsule is usually completed by cartilage medially (the *hiatus acusticus*) and ventrally. The *cavum* contains the membranous labyrinth of the inner ear. See *cavum labyrinthicum*, figs. 50-53, 87, 109.

CAVUM TYMPANI—A large concavity, opening laterally, in the posterior region of the skull; houses the tympanic organ (middle ear) and distalmost portion of the *columella auris*. The *incisura columellae auris* lies in the center of the *cavum tympani* and is in most cases the most medial portion of the *cavum*. Most of the *cavum* is formed by the quadrate with some contribution from the squamosal. The *antrum postoticum* is continuous with, and lies posterodorsal to, the *cavum*. See quadrate, fig. 132.

COLUMELLA AURIS—The bony rod (stapes) extending from the *fenestra ovalis* laterally across the *cavum acustico-jugulare* and through the *incisura columellae auris* into the *cavum tympani*. In most cases the lateral end is finished in cartilage, the extrastapes or extracolumella. This structure transmits sounds from the tympanic organ to the inner ear, see figs. 50, 87.

CONDYLUS MANDIBULARIS—The distal end of the *processus articularis* of the quadrate that articulates with the *area articularis mandibularis* of the lower jaw. See quadrate, fig. 10.

CONDYLUS OCCIPITALIS—The posteriorly projecting end of the occiput that articulates with the axis-atlas complex. See basioccipital and exoccipital, fig. 9, 66, 84-102.

CRISTA DORSALIS BASIOCCIPITALIS—The sagittal crest on the dorsal surface of the basioccipital just posterior to the *basis tuberculi basalis*. See basioccipital.

CRISTA PTERYGOIDEA—A vertical plate rising from the main body of the pterygoid, and sutured to the parietal dorsally. Together with the *processus inferior parietalis* it forms a lateral wall between the *cavum cranii* and the *fossa temporalis inferior*. See pterygoid, figs. 21-29.

CRISTA SUPRAOCCIPITALIS—The sagittal crest of the supraoccipital in the posterodorsal part of the skull. The parietal may contribute to this crest in some cases. The *adductor mandibulae externus*

musculature attaches along the crista. The *crista* may develop a posteriorly projecting spine and/or horizontal plate in some genera. See supraoccipital, figs. 9, 66, 104.

DORSUM SELLAE—A raised area in the center of the dorsal surface of the basisphenoid just posterior to the *sella turcica*. A *processus clinoides* extends anteriorly from each side. See basisphenoid, figs. 56, 60, 64.

FENESTRA OVALIS—The lateral opening of the *cavum labyrinthicum* into the *cavum acustico-jugulare*. The prootic forms the anterior border and the opisthotic the posterior border, whereas the ventral limits are formed by cartilage in life, but in the dried skull the *fenestra* is incomplete ventrally. In life, the *basis columellae* fits into and fills the *fenestra ovalis* and there is no free communication here between the *cavum labyrinthicum* and the *cavum acustico-jugulare*. See *cavum labyrinthicum*, figs. 11, 12, 50, 51.

FENESTRA PERILYMPHATICA—An opening between the *cavum labyrinthicum* and the *recessus scalae tympani* of the *cavum acustico-jugulare*, formed mostly by the *processus interfenestralis* of the opisthotic; may be completely contained within the opisthotic or may have a ventromedial contribution from the basioccipital. Baird (1960, fig. 49) indicated that the periotic sac of the inner ear extends posteriorly through this opening. See *cavum labyrinthicum*, figs. 48, 49, 52.

FENESTRA POSTOTICA—The posterior opening of the *cavum acustico-jugulare*; may be continuous laterally with the *incisura columellae auris* or medially with the *foramen jugulare posterius*; partially filled with cartilage in life; usually bordered by the exoccipital, quadrate, pterygoid, opisthotic, and sometimes the basioccipital. The following structures usually traverse the *fenestra postotica*: the stapedia artery, the lateral head vein, the vena cerebialis posterior, the glossopharyngeal (IX) nerve, the vagus (X) nerve, the accessory (XI) nerve and the hyomandibular branch of the facial (VII) nerve. The *fenestra* may be subdivided to a variable extent so that some or all of the above structures have their own foramen. See *cavum acustico-jugulare*, figs. 9, 84-102.

FENESTRA SUBTEMPORALIS—The ventral opening of the *fossa temporalis inferior*. The adductor jaw musculature, mandibular artery, and V₃ branch of the trigeminal nerve descend through this opening to the lower jaw. The quadrate, pterygoid, maxilla, jugal and quadratojugal form the margins of the *fenestra subtemporalis* in most cases, see fig. 9.

FISSURA ETHMOIDALIS—A fissure developed in the

midline of the posterior wall of the *fossa nasalis* above, and confluent with, the *sulcus vomeri* below; transmits the olfactory (I) nerves dorsally, ventrally filled with cartilage to form a canal for the nerves in life. Usually formed by prefrontal. See prefrontal, figs. 72-80.

FORAMEN ALVEOLARE INFERIUS—The posterior opening into the *canalis alveolaris inferior* in the dentary of the lower jaw; is in most cases in the posterior portion of the *sulcus cartilaginis meckelii* on the medial (internal) face of the mandible. See dentary, fig. 112.

FORAMEN ALVEOLARE SUPERIUS—The medial opening of the *canalis alveolaris superius* into the *fossa nasalis*; contains the *arteria alveolaris superior* (Albrecht, 1967); is in most cases formed by the maxilla. See maxilla, figs. 30-33.

FORAMEN ANTERIUS CANALIS CAROTICI INTERNI—Paired foramina in the dorsal surface of the basisphenoid in most cases opening at the posterior margin of the *sella turcica*. These foramina are the anterior openings of the *canalis carotici interni*. The medialmost branch of the *arteria carotica internus* enters into the *cavum cranii* here. See basisphenoid, figs. 30-33, 53-65.

FORAMEN ANTERIUS CHORDA TYMPANI—The anterior opening of the *canalis chorda tympani mandibularis* in the lower jaw; contains the chorda tympani branch of the facial (VII) nerve; opens into the *fossa meckelii* in *Chelydra* and is formed by the articular and prearticular bones. In *Podocnemis*, however, it opens on the medial face of the prearticular (Fuchs, 1931, pl. 2, fig. 5b). See prearticular, fig. 112.

FORAMEN AQUADUCTI VESTIBULI—A notch or foramen in the medioventral wall of the *cavum labyrinthicum* in the supraoccipital bone; opens into the *cavum cranii* and transmits the endolymphatic duct from the sacculus to the endolymphatic sac. See *cavum labyrinthicum*, figs. 52, 68, 69, 73, 74.

FORAMEN ARTERIAE ANTERIOVIANAE—A small opening on the dorsal surface of the pterygoid anterior to the anterior end of the *crista pterygoidea*, posteromedial to the dorsal *foramen palatinum posterius* in *Sternotherus* (Albrecht, 1967, p. 87), contains the anterior vidian artery in *Sternotherus*. See pterygoid, fig. 31.

FORAMEN ARTERIAEVIDIANAE—A series of "very small canals opening in the ventral surface of the palatine bone medial to the ventral foramen palatinum posterius . . ." (Albrecht, 1967, p. 87) in *Sternotherus*. A variable number of branches of the *arteria anterior vidianae* exit through these foramina to the roof of the mouth.

FORAMEN CAROTICO-PHARYNGEALE—A ventral opening (or series of openings) in the pterygoid connecting with the *canalis caroticus lateralis*. The *arteria carotico-pharyngealis* exits from the skull through this *foramen* (Albrecht, 1967, p. 86). See pterygoid, figs. 9, 33, 47.

FORAMEN CAROTICUM LATERALE—"In *Chrysemys*, *Sternotherus*, and *Trionyx*, the *canalis caroticus internus* on each side of the skull gives off an anterior canal [the *canalis caroticus lateralis*] in the pterygoid bone which opens into the *sulcus cavernosus* directly lateral to the basisphenoid" (Albrecht, 1967, p. 84). This opening is the *foramen caroticum laterale*, and in *Chrysemys* and *Sternotherus* (and most cryptodires) it carries the *arteria palatina*, whereas in *Trionyx* the *arteria mandibularis* passes through it. See pterygoid, figs. 30-33, 53-65.

FORAMEN CAVERNOSUM—The anterior opening of the *canalis cavernosus* into the *cavum cranii* proper; is thus placed between the *canalis cavernosus* and the *sulcus cavernosus*; traversed by the lateral head vein and, in most cryptodires, by the mandibular artery; usually formed by the pterygoid ventrally and the prootic dorsally. The posterior margin of the *foramen nervi trigemini* may also be the lateral margin of the *foramen cavernosum*. Thus, the *foramen cavernosum* is usually visible in anterolateral view through the *foramen nervi trigemini*. See pterygoid, figs. 21-29.

FORAMEN CHORDA TYMPANI INFERIUS—The ventral and lateral opening of the *canalis chorda tympani quadrati*; contains the chorda tympani branch of the facial (VII) nerve and usually occurs on the posterior face of the quadrate just below the *incisura columellae auris*. See quadrate, fig. 10, 107.

FORAMEN CHORDA TYMPANI SUPERIUS—The dorsal and medial opening of the *canalis chorda tympani quadrati* containing the chorda tympani branch of the facial (VII) nerve; is formed on the medial face of the quadrate near the *incisura columellae auris*. See quadrate, fig. 10, 107.

FORAMEN DENTOFACIALE MAJUS—An opening on the lateral surface of the lower jaw within the posterodorsal margin of the dentary; opens into a short canal (not named here) that extends antero-ventromedially into the *canalis alveolaris inferior*. I could not find a literature reference for the contents of this structure. See dentary, figs. 111, 112.

FORAMEN EXTERNUM NERVI GLOSSOPHARYNGEI—The opening containing the glossopharyngeal (IX) nerve as it enters the *cavum acustico-jugulare* in the dorsal portion of the *processus interfenestralis*

of the opisthotic. See *cavum acustico-jugulare* and *cavum labyrinthicum*, figs. 48, 51, 89, 90, 93, 94, 100.

FORAMEN INTERMANDIBULARIS CAUDALIS—A small opening between the ventral region of the *fossa meckelii* and the medial surface of the lower jaw. The *ramus intermandibularis caudalis* of the mandibular (V_3) nerve passes through this structure. The *foramen* is in most cases on the angular-prearticular suture but may not be completely surrounded by bone. See prearticular, fig. 112.

FORAMEN INTERMANDIBULARIS MEDIUS—The large anterior opening of the *fossa meckelii* on the medial surface of the lower jaw; is in most cases bounded posteriorly by the prearticular and anteriorly by the dentary. The *ramus intermandibularis medius* of the mandibular (V_3) nerve and in some cases (as in *Chelydra*) the meckelian cartilage are contained in the *foramen*. See dentary, fig. 112.

FORAMEN INTERMANDIBULARIS ORALIS—A small opening or notch communicating between the anterior region of the *fossa meckelii* and the medial surface of the lower jaw. The *ramus intermandibularis oralis* of the mandibular (V_3) nerve passes through this structure. The *foramen* is formed by the prearticular and angular in *Chelydra* but may be present only as a notch or indentation in the angular or prearticular. See prearticular, fig. 112.

FORAMEN INTERMAXILLARIS—An unpaired median opening found in the anterior region of the palate in *Carettochelys* and most trionychids. Formed primarily by the maxillae with contributions from the vomer and/or premaxillae in some forms. In *Carettochelys* the *foramen intermaxillaris* is apparently confluent with the *apertura narium interna*. See premaxilla, figs. 59, 174-185 (unlabeled).

FORAMEN INTERNUM NERVI GLOSSOPHARYNGEI—The opening at the point of exit of the glossopharyngeal (IX) nerve from the *cavum labyrinthicum* into a canal leading to the *foramen externum nervi glossopharyngei*. Both *foramina* are in the opisthotic. The *foramen internum* is absent when the glossopharyngeal passes to the outside without actually entering the *cavum labyrinthicum*. Ogushi (1911) showed the path of the glossopharyngeal (IX) nerve through the *cavum labyrinthicum* in *Trionyx* (fig. 105). See *Cavum labyrinthicum*, fig. 50.

FORAMEN INTERORBITALE—The paired openings between the orbits filled in life with cartilage; traversed by the optic nerves (II), portion of the eye muscles and the oculomotor (III), trochlearis

(IV), and a branch of the trigeminal (V) cranial nerves. Dorsally, the ridge defining the *sulcus olfactorius* forms a border for the *foramen interorbitale*. The following bones may take part in the formation of the *foramen interorbitale*: prefrontal, frontal, parietal, epipterygoid, pterygoid, palatine, and vomer, fig. 66.

FORAMEN JUGULARE ANTERIUS—The opening between the *cavum cranii* and the *recessus scalae tympani* portion of the *cavum acustico-jugulare* through which pass the vagus (X) and accessory (XI) nerves and the *vena cerebialis posterior* (or *vena jugularis* of mammals). The *foramen* is usually bounded anteriorly by the opisthotic and posteriorly by the exoccipital. See *cavum acustico-jugulare*, figs. 66-83.

FORAMEN JUGULARE POSTERIUS—An opening formed mostly by the exoccipital communicating between the *recessus scalae tympani* (a part of the *cavum acustico-jugulare*) and the outside of the skull; faces posteriorly and may be confluent with the *fenestra postotica* or completely absent; is traversed by the *vena cerebialis posterior* and in some cases by the vagus (X) and accessory (XI) nerves. See *cavum acustico-jugulare*, figs. 84-102.

FORAMEN MAGNUM—The large medial opening at the posterior end of the skull, opening posteriorly and placed just above the *condylus occipitalis*; transmits the spinal cord from the *cavum cranii* to the outside of the skull. The following bones may be involved in the formation of the *foramen magnum*: supraoccipital, exoccipital, and basioccipital, figs. 84-102.

FORAMEN MEDIALIS NERVI GLOSSOPHARYNGEI—The exit of the glossopharyngeal (IX) nerve from the *cavum cranii* occurs either in cartilage (the *hiatus acusticus*) or in bone; when ossified, this structure is usually found in the opisthotic. See *cavum labyrinthicum*, figs. 48-50.

FORAMEN NERVI ABDUCENTIS—The anterior and posterior openings of the *canalis nervi abducentis*. The abducent (VI) nerve enters and exits via these foramina in the basisphenoid. See basisphenoid, figs. 44, 53-65.

FORAMEN NERVI ACUSTICI—The *foramina*, in most cases in the *fossa acustico-facialis*, through which the branches of the acoustic (VIII) nerve exit from the *cavum cranii* and enter the *cavum labyrinthicum*. There are usually two *foramina* and these are formed by the prootic bone. See *cavum labyrinthicum*, figs. 67-83.

FORAMEN NERVI AURICULOTEMPORALIS—An opening (may be more than one) in the posterior portion of the lateral surface of the lower jaw containing

the auriculotemporalis nerve of Fuchs (1931) which appears to be the *ramus cutaneus recurrens* branch of the mandibular (V_3) nerve of Soliman (1964, fig. 15). The *foramen* or *foramina* are in most cases formed by the surangular bone. See surangular, fig. 111.

FORAMEN NERVI FACIALIS—The opening, in most cases in the *fossa acustico-facialis* in the prootic bone, through which the facial (VII) nerve exits from the *cavum cranii* and enters the *sulcus cavernosus*; may communicate with the *foramen pro ramo nervi vidiani*. (Note that I use this term for the opening visible in sagittal view [figs. 67-83] as well as the short canal [fig. 50] and more ventral opening into the *canalis cavernosus*, figs. 18, 37, 39). See prootic.

FORAMEN NERVI HYPOGLOSSI—The opening by which branches of the hypoglossal (XII) nerve leave the *cavum cranii*. The *foramina nervi hypoglossi* are in general formed by the exoccipital bone and in some cases by the basioccipital. See exoccipital, figs. 53-65, 67-83, 85-102.

FORAMEN NERVI TRIGEMINI—The opening between the *cavum cranii* and the *fossa temporalis inferior*, in most cases bordered, at least in part, by the prootic posteriorly, the pterygoid (and sometimes the epipterygoid) ventrally, and the parietal dorsally. Two branches (V_2 , V_3) of the trigeminal (V) nerve exit here along with the *arteria mandibularis* in most cryptodires (Soliman, 1964; Albrecht, 1967). Only the nerves exit in pleurodires. See prootic, figs. 11, 12, 66-83.

FORAMEN NERVI VIDIANI—Any opening in the *canalis nervi vidiani* into the *cavum cranii*. The palatine branch of the facial (VII) nerve (see Soliman, 1964) and various small arteries (see Albrecht, 1967) in most cases traverse this *foramen*. The *foramen* (or *foramina*) is usually formed by the pterygoid and/or palatine bones. See pterygoid, figs. 21, 28, 33, 53-55, 59.

FORAMEN ORBITO-NASALE—An opening between the *fossa nasalis* and the *fossa orbitalis* generally situated in the posteroventrolateral region of the *fossa nasalis*, transmits the posterior nasal artery from the *fossa orbitalis* to the *fossa nasalis* (Albrecht, 1967). The prefrontal, palatine, and maxilla in most cases participate in the formation of the *foramen orbito-nasale*. See palatine, figs. 9, 54-65.

FORAMEN PALATINUM ACCESSORIUM—In *Trionyx*, the ventral opening (actually a variable number of small *foramina*) of the *canalis intrapalatinus* in the palatine bone (Albrecht, 1967, p. 88). A small branch of the inframaxillary artery goes through the *canalis intrapalatinus* and exits

through these *foramina* to supply tissue on the roof of the mouth (Albrecht, 1967, p. 94).

FORAMEN PALATINUM POSTERIUS—An opening between the palatal surface of the skull and the area just behind the *fossa orbitalis* (pleurodires) or at the posteriormost limits of the *fossa orbitalis* (cryptodires); transmits the inframaxillary artery from the skull to the palate (Albrecht, 1967). The maxilla, palatine, and pterygoid may participate in the formation of the *foramen palatinum posterius*. See palatine, figs. 9, 53-64.

FORAMEN POSTERIUS CANALIS CAROTICI INTERNI—The most posterior opening of the *canalis caroticus internus*. The *arteria carotica interna* enters the *canalis* at this foramen; in most cryptodires the pterygoid forms the *foramen* but in baenoids it is formed by the basisphenoid and pterygoid. In pleurodires the *foramen* is usually formed by the prootic and sometimes the quadrate. See pterygoid and prootic, figs. 30-34, 85-101.

FORAMEN POSTERIUS CHORDA TYMPANI—The posterior opening of the *canalis chorda tympani mandibularis* in the lower jaw; contains the chorda tympani branch of the facial (VII) nerve. The *foramen* is formed by the articular and prearticular and occurs on the medial edge of the *area articularis mandibularis* in *Chelydra*. See prearticular, figs. 111, 112.

FORAMEN PRAEPALATINUM—Paired *foramina* in the anterior part of the palate that extend between the palate and *fossa nasalis*; transmit the anterior nasal artery from the palate into the nasal tissue (Albrecht, 1967, p. 94; Seydel, 1896); in most cases formed by the vomer and premaxilla. See premaxilla, figs. 9, 54, 55, 57, 58, 60, 63-65.

FORAMEN PRO RAMO NERVI VIDIANI—A short canal connecting the *canalis caroticus internus* with the *canalis cavernosus*; transmits the vidian nerve (palatine branch of VII) and a small branch of the internal carotid artery (Albrecht, 1967). The foramen is usually just ventral to the opening of the *foramen nervi facialis* into the *canalis cavernosus*. The *canalis nervi vidiani* in most cases extends anteriorly from the *foramen pro ramo nervi vidiani* and contains branches of the vidian nerve and blood vessels (Albrecht, 1967, p. 87). It is usually formed by the prootic and pterygoid. The *foramen* is apparently absent in pleurodires (see discussion under prootic). See pterygoid and prootic, figs. 24-29, 30-33.

FORAMEN STAPEDIO-TEMPORALE—The dorsal opening of the *canalis stapedio-temporalis* into the *fossa temporalis*. The *arteria stapedia* passes through this structure. The prootic and quadrate form the

- foramen stapedio-temporale*. See prootic and *cavum acustico-jugulare*, figs. 10, 30-33, 56, 57.
- FORAMEN SUPRAMAXILLARE**—An opening in the maxilla in the floor of the *fossa orbitalis*; *foramen supramaxillare* leads into the *canalis infraorbitalis* and transmits the *arteria supramaxillaris* (Albrecht, 1967). See maxilla, figs. 30-33, 54, 56-59, 63, 65.
- FORAMEN SUPRAORBITALE**—An "extremely small arterial foramen . . . located on the prefrontal bone in the anterodorsal part of the orbit, dorsolateral from the dorsal edge of the *fissura ethmoidalis*" (Albrecht, 1967, p. 88); contains a branch of the *arteria supraorbitalis* (*ibid.*). See figs. 30-32.
- FOSSA ACUSTICO-FACIALIS**—A depression in that part of the prootic that forms the lateral wall of the *cavum cranii*. There are usually three *foramina* in this fossa: the *foramen nervi facialis* and two *foramina nervi acustici*. The fossa contains the *ganglion vestibulare* (Soliman, 1964). See prootic and *cavum labyrinthicum*, figs. 66-83.
- FOSSA CARTILAGINIS EPIPTERYGOIDEI**—The space between the posteroventral process of the epipterygoid (or parietal if epipterygoid is absent) and the *processus epipterygoideus* of the quadrate which is occupied in life by a remnant of the palatoquadrate cartilage. The limits of the fossa are usually formed by the quadrate, pterygoid, and epipterygoid (or parietal). See quadrate, pterygoid, and epipterygoid, fig. 13.
- FOSSA MECKELII**—In the lower jaw, a space behind the *processus coronoideus* and anterior to the jaw articulation that is open dorsally and communicates anteriorly with the *sulcus cartilaginis meckelii*. Schumacher (1954, 1955a, 1955b) reported muscle fibers of the *M. pseudotemporalis* and *M. adductor mandibulae posterior* in the *fossa meckelii*. See dentary and prearticular, figs. 111, 112.
- FOSSA NASALIS**—The large, median cavity at the very front of the skull, anterior and median to the *fossa orbitalis*. This cavity houses the nasal capsules and cavities. The nasal (when present), prefrontal, maxilla, premaxilla, and vomer usually participate in the formation of this fossa, figs. 53-64, 66-83 (unlabeled).
- FOSSA ORBITALIS**—The bony socket for the eye, usually poorly defined and open to the *fossa temporalis*, *cavum cranii*, and *fossa nasalis*. The following bones usually form parts of the *fossa orbitalis*: prefrontal, maxilla, jugal, palatine, postorbital, and parietal, figs. 53-64 (unlabeled).
- FOSSA TEMPORALIS INFERIOR**—The space below the level of the otic chamber and anterior to it and continuous with the *fossa temporalis superior*; contains the *M. adductor mandibulae internus*, part of the *M. adductor mandibulae externus*, and the *M. pterygoideus*. Parietal, postorbital, jugal, maxilla, quadratojugal, pterygoid, epipterygoid (when present) prootic, and quadrate in most cases are involved in forming the *fossa temporalis inferior*. See fig. 9.
- FOSSA TEMPORALIS SUPERIOR**—The space above and behind the otic chamber and below the temporal roof (if present); contains the main mass of the *M. adductor mandibulae externus*. The following bones usually form the boundaries of the *fossa temporalis superior*: supraoccipital, parietal, prootic, opisthotic, quadrate, squamosal, postorbital, and exoccipital.
- HIATUS ACUSTICUS**—The large, irregular opening between the *cavum cranii* and the *cavum labyrinthicum*; in life is occupied by a cartilaginous wall; in some forms may be ossified. The following bones in most cases form the margins of the *hiatus acusticus*: supraoccipital, prootic, basisphenoid, basioccipital, and opisthotic. Siebenrock (1897, figs. 1-9) illustrated variable conditions of ossification of the bones surrounding the *hiatus acusticus*. See *cavum labyrinthicum*, figs. 66-80.
- HIATUS POSTLAGENUM**—An opening connecting the *cavum labyrinthicum* and the *recessus scalae tympani*. Dorsally it is formed by the ventral edge of the *processus interfenestralis* of the opisthotic and ventrally by the basioccipital. The term is modified from "postlagenar hiatus" of McDowell (1964) and is presumably equivalent to the *canalis hypoperilymphaticus* of Versluys (1936) and the *ductus hypoperilymphaticus* of Nick (1912) and deBeer (1937). See *cavum acustico-jugulare*, fig. 48.
- INCISURA COLUMELLAE AURIS**—The groove or canal within the quadrate which contains the *columella auris*. In some turtles the *incisura* also contains the eustachian tube. See quadrate, figs. 10, 90-101.
- MEATUS CHOANAE**—A tunnel or tube connecting the *fossa nasalis* and the *apertura narium interna*, not developed in most turtles. See maxilla.
- PROCESSUS ARTICULARIS**—The ventral process of the quadrate that bears the actual articulation with the lower jaw; the *condylus mandibularis*. See quadrate, fig. 10.
- PROCESSUS CLINOIDEUS**—Paired anterolateral spines on the basisphenoid, generally on either side of the *dorsum sellae*. The *canalis nervi abducentis* in most turtles penetrates the base of the *processus*. See basisphenoid, figs. 53-65, 69, 72, 76-80.
- PROCESSUS CORONOIDEUS**—A dorsally directed proc-

ess of the lower jaw generally developed on the coronoid bone; is found between the triturating surface and the *fossa meckelii*. Fibers of the *M. adductor mandibulae externus* attach on the *processus* along with the main external adductor tendon (Schumacher, 1954, 1955a, 1955b). See coronoid, fig. 111.

PROCESSUS EPIPTERYGOIDEUS—An anterior extension of the quadrate, generally found below the *foramen nervi trigemini* in the *fossa subtemporalis*; process generally extends toward the epipterygoid or a ventral extension of the parietal if the epipterygoid is absent. See quadrate, figs. 10, 51.

PROCESSUS INFERIOR PARIETALIS—The ventral process of the parietal that forms a lateral wall for the *cavum cranii*; the *processus* generally has an extensive ventral contact with the *crista pterygoidea* and forms part of the lateral wall between the *cavum cranii* and the *fossa temporalis*. See parietal and *cavum epiptericum* (pterygoid), figs. 18, 19, 66-82.

PROCESSUS INTERFENESTRALIS—A ventral process of the opisthotic extending into the *cavum acustico-jugulare* and separating the *cavum* into two parts, lateral and posterior, the latter being the *recessus scalae tympani*. The *foramen internum nervi glossopharyngei* and *foramen externum nervi glossopharyngei* generally penetrate the dorsal portion of the process. The anterior surface of the *processus* walls the *cavum labyrinthicum*. See *cavum acustico-jugulare* and *cavum labyrinthicum*, figs. 11, 12, 18, 19, 49, 84-102.

PROCESSUS PAROCCIPITALIS—The posterolateral process of the opisthotic that contacts the quadrate and squamosal laterally. See opisthotic, figs. 42, 43, 49.

PROCESSUS PTERYGOIDEUS EXTERNUS—The lateral process of the pterygoid in cryptodires that extends around the anteromedial edge of the *fossa temporalis inferior* and may extend into the *fossa*. The lateral edge is generally produced into a vertical plate that acts as a guide for the lower jaw during adduction of the lower jaw. See pterygoid, figs. 9, 53-65.

PROCESSUS TROCHLEARIS OTICUM—The extension or area on the otic chamber developed for an articular facet with the *cartilago transiliens*; it is generally borne mostly by the quadrate with a smaller contribution from the prootic, and found only in cryptodires. See prootic, figs. 11, 14.

PROCESSUS TROCHLEARIS PTERYGOIDEI—A lateral extension of the pterygoid into the *fossa temporalis inferior* which supports the *cartilago transiliens*; the *processus* is generally convex outward or forward and is found only in pleurodires. Bears

modified *mundplatte*. See pterygoid, figs. 12, 14, 53-55.

RECESSUS LABYRINTHICUS OPISTHOTICUS—A hemispherical cavity off the *cavum labyrinthicum* in the opisthotic that houses the posterior ampulla and the union of the posterior and horizontal semicircular canals. See *cavum labyrinthicum*, figs. 49, 52.

RECESSUS LABYRINTHICUS PROOTICUS—A hemispherical cavity off the *cavum labyrinthicum* in the prootic that houses the ampullae of the anterior and horizontal semicircular canals. See *cavum labyrinthicum*, fig. 52.

RECESSUS LABYRINTHICUS SUPRAOCCIPITALIS—A variously shaped cavity off the *cavum labyrinthicum* in the supraoccipital that houses the union of the anterior and posterior semicircular canals. See *cavum labyrinthicum*, fig. 52.

RECESSUS SCALAE TYMPANI—That portion of the *cavum acustico-jugulare* lying roughly posterior to the *processus interfenestralis* of the opisthotic. The vagus (X) and accessory (XI) nerves and the *vena cerebialis posterior* traverse the posterior part of the chamber. Most of the *recessus* is filled by the periotic sac (Baird, 1960) and it is usually formed by the pterygoid, opisthotic, exoccipital, and basioccipital. See *cavum acustico-jugulare*, figs. 48-51.

ROSTRUM BASISPHENOIDALE—The anterior elongation of the basisphenoid anterior to the *sella turcica*. See basisphenoid, figs. 53-65, 67-80.

SELLA TURCICA—The pit or depression in the anterior part of the dorsal surface of the basisphenoid that houses the pituitary. See basisphenoid, figs. 53-65, 67-80.

SULCUS CARTILAGINIS MECKELII—A medially concave groove on the inside of the dentary bone of the lower jaw extending anteriorly from the *fossa meckelii*. See dentary, fig. 112.

SULCUS CAVERNOSUS—A long trough lying on the floor of the *cavum cranii* medial to the *crista pterygoidea* on the pterygoid and lateral to the *rostrum basisphenoidale*; begins at the anterior opening of the *canalis cavernosus* and continues anteromedially. The *vena capitis lateralis* travels along the *sulcus*. See pterygoid, figs. 21-29.

SULCUS OLFACTORIUS—A ventrally open median trough extending from the *cavum cranii* into the *fossa nasalis*; carries the olfactory (I) nerve to the nasal capsule. The *sulcus* is usually formed by the prefrontal, frontal and parietal. See frontal, figs. 66-80.

SULCUS VOMERI—A dorsally open, median groove extending posteriorly from the *fossa nasalis* and formed by the vomer; supports the cartilaginous

septum nasalis (Soliman, 1964, figs. 12, 23). See vomer, figs. 72-80.

TUBERCULUM BASIOCCIPITALE—Paired posterolateral processes formed on the ventral surface of the basioccipital. See basioccipital, fig. 9.

ACKNOWLEDGMENTS

I have been fortunate to have an English translation of Siebenrock (1897) and some other papers prepared for me by Miss Barbara Werscheck, who also typed the manuscript and checked many of the references. I also thank Dr. Michael Cluver who translated an Afrikaans article. Miss Charlotte Holton obtained references and specimen data. Nearly all the new illustrations are the work of Miss Lorraine Meeker, who, in addition to checking sutures and preparing high quality illustrations, continuously drew what she saw rather than what it should have looked like. Mr. Chester S. Tarka

took some of the photographs and generally aided in all the work on the figures. I am grateful to Drs. Dennis Bramble, John Legler, Richard Moody, Ernest Williams, Roger Wood, Rainer Zangerl and Dr. David Archibald for generously giving me access to their unpublished work and/or illustrations.

Because of the scope of this article virtually every institution and collection that I have visited supplied something of value, but I do not think it would be worth listing them all here. Most of the Recent skulls I examined are from the American Museum of Natural History, Department of Herpetology collections where I was often helped by Dr. Richard Zweifel and Mr. George Foley. The manuscript was read in an earlier form by Drs. Philip Albrecht and Samuel B. McDowell, both of whom took time to make extensive constructive comments and I appreciate their help.

INDEX TO GENERA

For references to subjects see Contents (bones) and Glossary (anatomical terms).

Adelochelys, p. 299
Adocus, fig. 171; p. 91
Allopleuron, p. 292
Amyda, pp. 240, 243, 245
Annamemys, p. 299
Anosteira, fig. 173
Apertotemporalis, p. 326
Archelon, fig. 190; pp. 90, 281
Argillochelys, p. 292
Aspideretes, p. 243
Aspilus, p. 242
Astrochelys, p. 324

Baena, figs. 71, 153; pp. 73, 75, 233
Baptemys, pp. 91, 120, 205, 236
Bartlettia, p. 230
Basilemys, p. 236
Batagur, figs. 96, 225, 265; pp. 85, 87, 91, 94, 213, 299, 301, 302
Batrachemys, fig. 142; pp. 86, 102, 230, 231
Bellia, p. 302
Bothremys, figs. 125, 126, 127; pp. 73, 74, 80, 89, 93, 97, 115, 210, 213, 228, 229, 230

Callagur, fig. 226
Callinia, p. 242

Captorhinus, pp. 81, 109, 204, 207
Caretta, figs. 199, 200, 214, 215, 216; pp. 82, 88, 90, 92, 112, 191, 218, 292
Carettochelys, figs. 91, 174, 175; pp. 76, 79, 82, 85, 87, 91, 92, 93, 94, 96, 97, 99, 108, 110, 114, 137, 211, 212, 220, 237, 360
Chelymys, p. 231
Chelodina, figs. 19, 44, 52, 110, 143; pp. 72, 76, 78, 80, 81, 82, 85, 102, 105, 106, 109, 120, 126, 213, 230, 231
Chelone, pp. 106, 292
Chelonia, figs. 26, 44, 62, 82, 199, 214, 215; pp. 76, 77, 90, 97, 98, 100, 132, 136, 173, 214, 218, 285, 287, 289, 292
Chelonoidis, fig. 258; p. 324
Chelosphargis, fig. 191; p. 281
Chelus, figs. 23, 70, 88, 144, 150; pp. 72, 77, 80, 82, 85, 86, 87, 88, 89, 90, 92, 93, 100, 102, 105, 108, 109, 115, 137, 144, 210, 213, 214, 216, 217, 230, 231
Chelydra, figs. 9, 10, 11, 16, 18, 20, 27, 33, 34, 37, 39, 41, 42, 49, 50, 51, 64, 76, 81, 87, 95, 111, 112, 199, 217, 218; pp. 71, 76, 82, 85, 90, 91, 93, 94, 98, 101, 103, 110, 111, 115, 121, 126, 136, 137, 172, 173, 190, 191, 214, 217, 218, 220, 223, 285, 293, 294, 295, 296, 297, 356, 359, 360, 361
Chersina, pp. 324, 326
Chersinella, p. 324

- Chinemys*, figs. 79, 227, 256; pp. 91, 94, 101, 299, 322
- Chisternon*, figs. 1, 3, 13, 94, 154, 155; pp. 72, 75, 233
- Chitra*, fig. 176; pp. 73, 74, 91, 92, 238, 242, 243, 245, 326
- Chitracephalus*, p. 326
- Chrysemys*, figs. 28, 30, 65, 66, 78, 97, 228, 229, 230, 255, 257; pp. 77, 79, 80, 81, 85, 90, 93, 98, 101, 102, 103, 136, 215, 218, 223, 299, 301, 302, 303, 322, 356, 357, 359
- Cinosternum*, p. 237
- Cistudo*, p. 302
- Claudius*, figs. 165, 170; pp. 85, 132
- Clemmys*, figs. 2, 47, 48, 231; pp. 85, 101, 211, 299, 302, 303, 322
- Colpochelys*, p. 292
- Corsochelys*, fig. 206; pp. 85, 110, 114, 289, 292
- Crossochelys*, fig. 268; pp. 81, 83, 107, 326
- Ctenochelys*, figs. 198, 199; pp. 90, 285
- Cuora*, fig. 232; pp. 80, 81, 299, 302, 322
- Cyclanorbis*, figs. 92, 117, 178; pp. 92, 212, 242, 243
- Cyclanosteus*, p. 242
- Cyclemys*, pp. 95, 127, 132, 173, 299, 322
- Cycloderma*, fig. 179; pp. 73, 78, 87, 92, 212, 216, 242, 243
- Dacquemys*, fig. 128; pp. 229, 230
- Damonia*, pp. 299, 302, 322
- Deirochelys*, figs. 233, 255; pp. 79, 91, 94, 212, 299
- Dermatemys*, figs. 58, 73, 90, 172; pp. 79, 85, 87, 91, 94, 95, 120, 205, 211, 212, 213, 220, 234, 237
- Dermochelys*, figs. 61, 83, 102, 201, 202, 203, 204; pp. 76, 79, 81, 82, 84, 85, 87, 88, 89, 90, 93, 94, 96, 98, 99, 102, 107, 108, 110, 115, 135, 136, 137, 173, 213, 216, 217, 218, 219, 220, 223, 285, 287, 293
- Desmatochelys*, figs. 207, 208; pp. 85, 292, 293
- Dogania*, pp. 75, 238, 242, 245
- Dorsetochelys*, p. 233
- Echmatemys*, p. 302
- Elseya*, fig. 55; pp. 86, 137, 230, 231
- Emydoidea*, p. 299
- Emydura*, figs. 12, 38, 40, 43, 69, 145, 150; pp. 73, 75, 80, 86, 89, 114, 123, 137, 212, 230, 231
- Emys*, figs. 52, 234; pp. 76, 77, 80, 91, 93, 98, 99, 106, 136, 204, 223, 297, 299, 301, 302, 303, 322
- Eochelone*, fig. 209; p. 292
- Eosphargis*, fig. 205; pp. 90, 287
- Eretmochelys*, figs. 75, 199, 214, 215, 216; pp. 90, 97, 106, 121, 173, 218, 223, 289, 292
- Erquellinnesia*, figs. 194, 195, 196, 199, 200; pp. 84, 90, 92, 93, 214, 285
- Erymnochelys*, figs. 129, 139, 140, 141; pp. 78, 81, 85, 87, 96, 102, 124, 213, 228, 230
- Eubaena*, figs. 1, 34, 56, 156, 157, 158; pp. 75, 79, 90, 233, 234
- Eurycephalochelys*, fig. 180; p. 243
- Fordia*, p. 242
- Geochelone*, figs. 6, 29, 80, 99, 258, 265, 266; pp. 76, 82, 87, 88, 91, 92, 93, 94, 98, 100, 101, 104, 108, 132, 135, 137, 145, 173, 213, 322, 324, 326
- Geoclemys*, fig. 235; pp. 85, 299, 322
- Geoemyda*, fig. 236; pp. 78, 79, 80, 85, 127, 299, 322
- Glarichelys*, p. 292
- Glyptemys*, p. 302
- Glyptops*, figs. 1, 151; pp. 84, 88, 90, 213, 234
- Gopherus*, figs. 2, 15, 98, 259, 267; pp. 78, 101, 132, 172, 322, 324, 326
- Graptemys*, figs. 237, 254; pp. 91, 101, 299, 303
- Hangaemys*, p. 327
- Hardella*, figs. 238, 257; pp. 90, 302, 303
- Hayemys*, figs. 1, 159; pp. 233, 234
- Heosemys*, pp. 80, 127, 299, 322
- Heptathyra*, p. 242
- Hesperotestudo*, p. 213
- Hieremys*, fig. 239; pp. 80, 85, 299, 322
- Homopus*, fig. 260; pp. 324, 326
- Hydraspis*, pp. 86, 230, 231
- Hydromedusa*, figs. 146, 150; pp. 92, 93, 213, 231
- Iguana*, p. 106
- Isola*, p. 242
- Kachuga*, figs. 240, 241, 242; pp. 299, 301, 302
- Kallokibotion*, pp. 73, 87, 327
- Kinixys*, fig. 261; pp. 83, 91, 322, 324, 326
- Kinosternon*, fig. 166; pp. 93, 100, 101, 237
- Lepidochelys*, figs. 101, 210, 211, 215; p. 292
- Lissemys*, figs. 181, 186; pp. 101, 145, 238, 240, 242, 243
- Macrobaena*, p. 327
- Macrocephalochelys*, p. 296
- Macrochelys*, p. 297
- Macrolemys*, figs. 44, 52, 77, 219, 220, 224; pp. 87, 88, 91, 101, 103, 126, 213, 295, 296, 297
- Madakinixys*, p. 326
- Malaclemys*, figs. 243, 254; pp. 79, 81, 91, 112, 113, 114, 137, 299, 302
- Malacochersus*, figs. 262, 267; p. 326

- Malayemys*, fig. 244; pp. 79, 94, 299, 301, 302, 322
Mauremys, figs. 47, 48, 245, 255; pp. 211, 299, 302, 303, 322
Meiolania, figs. 268, 269; p. 338
Melanochelys, fig. 246; pp. 80, 299, 302
Mesochelys, fig. 152; p. 233
Mesoclemys, fig. 147
Morenia, fig. 247; p. 299
- Nanemys*, p. 322
Nanhsiungchelys, fig. 270; p. 338
Nicoria, pp. 85, 322
Nilssonina, p. 242
Niolamia, fig. 268; pp. 83, 338
Notochelys, p. 80
- Ocadia*, fig. 248; pp. 101, 299, 302
Onychochelys, pp. 292
Orlitia, fig. 249; pp. 299, 322
Osteopygis, figs. 198, 200; pp. 90, 285
- Palatobaena*, figs. 160, 161; pp. 73, 84, 90, 233
Pelochelys, figs. 93, 182, 186; pp. 78, 91, 92, 94, 115, 136, 137, 213, 238, 240, 242, 243, 245
Pelomedusa, figs. 21, 45, 130; pp. 85, 102, 110, 114, 122, 123, 215, 228, 229, 230
Peltastes, p. 324
Peltocephalus, figs. 131, 139, 141; pp. 78, 81, 85, 102, 228, 230
Pelusios, figs. 4, 34, 53, 67, 85, 132, 133; pp. 73, 75, 85, 102, 110, 114, 123, 212, 228, 230
Phrynops, pp. 86, 92, 213, 230, 231
Plastomenus, fig. 183
Platemys, figs. 148, 150; pp. 86, 92, 102, 213, 231
Platypeltis, pp. 243, 245
Platysternon, figs. 63, 221, 222, 224; pp. 78, 79, 81, 82, 84, 85, 87, 91, 93, 218, 220, 294, 295
Plesiobaena, fig. 162, p. 233
Plesiochelys, figs. 100, 187, 188; pp. 84, 108, 137, 281
Podocnemis, figs. 5, 8, 17, 22, 46A, 46B, 54, 68, 86, 134, 135, 139, 140; pp. 78, 80, 81, 82, 83, 85, 89, 92, 95, 96, 97, 101, 102, 105, 106, 108, 109, 110, 111, 113, 114, 127, 136, 140, 172, 190, 210, 213, 216, 217, 218, 225, 228, 229, 230, 359
Portochelys, p. 285
Portlandemys, figs. 60, 189; pp. 96, 281
Potamochelys, pp. 229, 242
Proganochelys, figs. 114, 115, 116, 117, 118, 119, 120, 121, 122, 124; pp. 72, 75, 82, 87, 88, 89, 96, 100, 207, 210, 212, 225
Protochelydra, fig. 223; pp. 91, 295
Protostega, figs. 192, 193; p. 281
- Psammobates*, figs. 52, 266; p. 326
Psephophorus, p. 287
Pseudanosteira, fig. 173
Pseudemydura, figs. 89, 149; pp. 78, 80, 82, 85, 86, 230, 231
Pseudemys, figs. 150, 228, 229, 257; pp. 103, 299, 301, 302, 322
Ptychogaster, pp. 85, 299
Puppigerus, fig. 212, p. 292
Pyxis, fig. 263; pp. 324, 326
- Rafetus*, p. 242
Rhetechelys, p. 285
Rhinemys, p. 230
Rhinochelys, pp. 72, 90, 281
Rhinoclemys, figs. 52, 250; pp. 80, 322
Roxochelys, p. 229
- Sacalia*, pp. 211, 299
Scutemys, p. 338
Shweboemys, figs. 136, 137; pp. 89, 230
Siebenrockiella, fig. 251; pp. 299, 302, 322
Sinemys, p. 338
Solnhofia, figs. 57, 271, 272, 273; pp. 72, 96, 115, 326, 338
Sphargis, p. 287
Staurotypus, fig. 167; pp. 76, 91, 94, 217, 237
Stegochelys, p. 225
Stereogenys, pp. 214, 228, 229
Sternotherus, figs. 31, 44, 72, 168, 170; pp. 93, 101, 102, 230, 237, 356, 357, 359
Stygiocichelys, figs. 1, 163; p. 233
Stylemys, pp. 322, 324
- Taphrosphys*, fig. 138; pp. 97, 110, 114
Terrapene, figs. 252, 253, 255; pp. 79, 81, 85, 95, 101, 107, 120, 137, 217, 299, 301, 322
Testudo, figs. 264, 265, 266; pp. 78, 82, 95, 101, 115, 132, 172, 173, 322, 324, 326
Tetraonyx, p. 302
Toxochelys, figs. 197, 198; pp. 84, 90, 285
Trachemys, p. 302
Triassochelys, p. 87
Trinitichelys, fig. 164; pp. 84, 233
Trionyx, figs. 25, 32, 52, 59, 74, 103, 104, 105, 107, 184, 185; pp. 74, 75, 85, 88, 89, 91, 93, 94, 98, 100, 101, 103, 104, 113, 114, 173, 190, 191, 211, 212, 220, 238, 240, 242, 243, 245, 356, 357, 359, 361
- Varanus*, p. 106
- Xenochelys*, fig. 169; pp. 91, 234, 237
Xerobates, p. 324

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